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THE PLANT RUSTS

(UREDINALES)

BY

JOSEPH C. ARTHUR

IN COLLABORATION WITH

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PREFACE

The present volume is the outgrowth of work begun and conducted for many years under the direction of the senior author in the botanical laboratories of the Agricultural Experiment Station of Purdue University at Lafayette, Indiana. The early work was done in the eighties and nineties, but the more active period has been the last twenty years during which time the rust-flora of North America has been intimately studied. The taxonomic results of this work have been published in the seventh volume of the North American Flora.

The book was planned to present a general account of the rusts, particularly of a biologic nature, in the light of the ideas and conceptions emanating from the laboratory that could not find place in the work referred to, and have found only partial expression in fragmentary form in occasional papers by different members of the staff.

A work in which so many persons have volunteered to collaborate necessarily raised various problems pertaining to gathering of data, making interpretations, evolving plans for presentation, and finally the preparation of manuscript. These difficulties were considerably increased by the separation of the group of collaborators, most of whom severed their active connection with the laboratory several years since. The preparation of the different portions of the manuscript was mostly undertaken at the various places of residence. In order to bring the separate pieces of writing into a connected presentation many changes in the original drafts were necessary. Each author criticized the writing of the others, both as to content and wording, and changes were made from time to time as the work progressed. The responsibility for bringing all matters into final form, however, has devolved upon the senior author.

It is needless, perhaps, to point out that a book conceived and written in this manner can not take the form of presentation or diction of any one of its authors. It is a composite piece of work representing the product of a laboratory over a long period of years, and it is not to be assumed that all details accord with the views of each of the contributors. In fact there remain here and there occasional statements which are not endorsed by one or more of the several authors. In spite of the inevitable fact that divergent opinions and tendencies exist

it is thought best to present the volume in its present form rather than as a collection of essays by the different collaborators.

A few words of explanation regarding the treatment of the subject may be helpful. In the first chapter the authors have undertaken to give an outline of the structure and habits of the rusts, using technical terms as sparingly as possible, desiring to make a simple, concise and readable presentation. The chapters which follow deal in a more extended way with the several subdivisions of the subject. In no case, however, has any approach been made to a monographic treatment, and consequently many interesting topics have been omitted or briefly mentioned, the citation of literature is limited, and the discussion of deductions and theoretical questions has been pursued only to an extent that would help to bind together the underlying facts.

The authors are greatly indebted to Dr. B. O. Dodge, lately of the Bureau of Plant Industry, Washington, D. C., Dr. E. C. Stakman of the University of Minnesota, and Mr. J. Ramsbottom of the Natural History Department of the British Museum, who read portions of the manuscript and kindly offered helpful suggestions. Thanks are also due to Professor J. H. Faull, lately of the University of Toronto, Professor H. H. Whetzel of Cornell University, Dr. H. B. Humphrey of the United States Bureau of Plant Industry, Dr. E. Gäumann of the Schweizerische landwirtschaftliche Versuchsanstalt, Zürich, Switzerland, and Professor H. Klebahn, of the Botanisches Staatsinstitut, Hamburg, Germany, for assistance in various ways, as well as to many other botanists both in Europe and America. To Miss Jessie M. Allen, Librarian of the United States Bureau of Plant Industry, who verified the references in the literature cited, much credit is due for their accuracy. To the Division of Biology and Agriculture of the National Research Council, to the Office of Cereal Investigations in the United States Bureau of Plant Industry, and especially to the Agricultural Experiment Station of Purdue University very grateful acknowledgment is made for financial assistance and for a warm interest in the project, without which the work might not have been started and could not have been maintained. The several institutions with which the authors were connected during the preparation of the work — Pennsylvania State College, Purdue University, Virginia Polytechnic Institute and Manitoba Agricultural College — have also extended courtesies in aid of the project.

THE AUTHORS.

January 1, 1929

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THE PLANT RUSTS

CHAPTER I

THE GENERAL NATURE OF THE RUSTS

Vegetative and reproductive parts: the cycle of development, macrocyclic and microcyclic forms, relation to host.
The sorus and its spores in macrocyclic species: structure of the sorus, accessory parts, succession of sori, pycnia, aecia, uredinia, telia.
The sorus and its spores in microcyclic species: pycnia, microtelia.
The basidium and basidiospores.
Life-cycles illustrated: macrocyclic rusts, uredinia unlike aecia, uredinia resembling aecia; microcyclic rusts; mutable species.
Rusts in relation to other fungi; importance of the group; habitat and distribution.
Literature.

VEGETATIVE AND REPRODUCTIVE PARTS

The rusts, more distinctly designated as plant rusts, rust-fungi or Uredinales, are small, mostly microscopic fungi, parasitic in the tissues of ferns and seed-plants. Like most other fungi they possess a vegetative part, known as the mycelium, which gives rise to the reproductive structures, the sori. All rusts are obligate parasites, that is, they are strictly parasitic and live within the tissues of their hosts. The mycelium consists of long, branching, septate threads, or hyphae. The hyphae spread through the living parts of the host by forcing their way along the cell-walls in the middle lamella (Fig. 1 *a*), or through the intercellular spaces, or follow the surface of the cells within the plant when these are not in contact. The nutriment for the rust is secured in part or wholly by means of haustoria, which are globoid, elongate, or more or less branched organs (Fig. 1 *b*). They arise from the hyphae and extend into the interior of the cells.

Reproduction is brought about by the massing of mycelium in certain definite parts of the host where sori are developed (Fig. 2). These sori give rise to the spores, which have varied forms and functions to meet the different requirements of continued existence.

The cycle of development. — Every rust during its life period normally goes through a certain succession of fundamental changes,

which constitute the life-cycle, or complete cycle of development (Figs. 3 and 4). This cycle is divided into two unlike and distinct phases, which may be regarded as gametophytic or haploid and sporophytic or diploid, although these terms are not strictly applicable.[1]

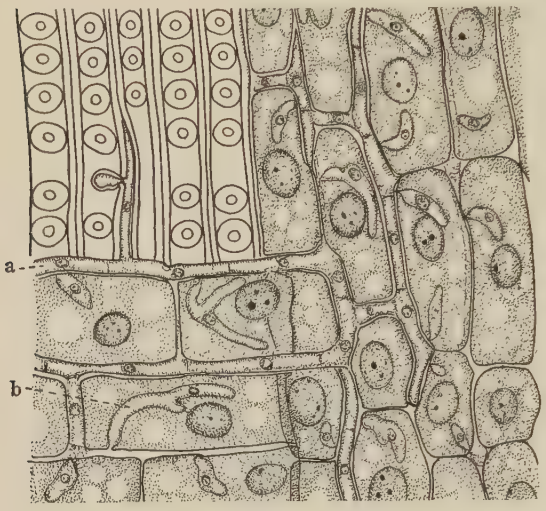

FIG. 1. — Relation of mycelium to its host: *Cronartium ribicola* in stem of *Pinus strobus;* *a* hyphae passing above and at the right between the cells of the parenchyma with their large nuclei, and at the left passing between the tracheids with their large bordered pits, each cell of the hyphae with a nucleus; *b* haustoria of various shapes, each with a nucleus. The nuclei of the host-cells are very much larger than the nuclei of the fungus. (After Colley, 1918.)

The mycelium both of the gametophytic phase and of the sporophytic phase, arises in the majority of species from the germination of a spore, and consequently in such cases the mycelium of one phase never continues into that of the other. In some species, however, there is a shorter life-cycle in which no mycelium is produced in the sporophytic generation.

MACROCYCLIC AND MICROCYCLIC FORMS. — It is well to bear in mind that the vegetative body of the rust-fungus is the mycelium, and that the spores are its reproductive structures. When mycelium occurs both in the gametophytic and the sporophytic phases of its existence

[1] The term gametophytic is used because it is assumed that the mycelium in this stage, either now produces or at some early ancestral period was capable of producing gametes, or their equivalents. The term haploid is sometimes preferred because the cells of the mycelium and spores of this stage are usually uninucleate, and hence contain the haploid or reduced number of chromosomes. The term sporophytic is used for the second phase because this phase is spore-bearing and is considered to be non-sexual. It is also called the diploid phase because the cells of both mycelium and spores are usually binucleate, and hence contain the diploid or double number of chromosomes. These terms are taken from higher plants, and they do not apply strictly to the rusts. However, they are convenient and suggestive terms, and sufficiently accurate to serve present purposes.

(Fig. 3), the rust is macrocyclic (long-cycle), as in the cereal rust *Puccinia graminis*, but when it occurs only in the gametophytic phase (Fig. 4), the rust is microcyclic (short-cycle), as in the hollyhock rust *Puccinia malvacearum*.

Since the macrocyclic rusts have two independent mycelial bodies while completing a cycle of their existence, and are conceived to be the more primitive, and since they are capable of producing more kinds of spores than the microcyclic rusts, they will be described first. Microcyclic species are considered on page 21.

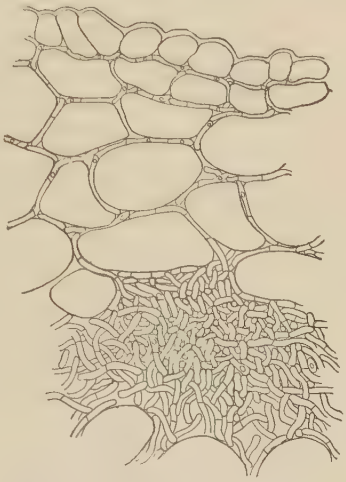

Fig. 2. — Primordium of a sorus, formed between the cells of parenchyma in a leaf of *Abies balsamea;* very early stage of the aecium of *Uredinopsis mirabilis* (*Peridermium balsameum*). (After Adams, 1919.)

Relation to host. — A limited choice of nearly related hosts for a part or all of the life-cycle of each species is characteristic of the rusts, and indicates their highly parasitic nature. When the sporophytic phase exists upon the same species of host or a closely related one as that bearing the gametophytic phase, the condition is known as autoecism. Autoecious rusts, therefore, are restricted to more or less closely related species. In some instances, however, and especially with certain groups of rusts, the aeciospores do not infect the same or nearly related host which bears them, but do infect a most unlike and distantly related host, as in *Puccinia graminis*, which has the gametophytic phase of its mycelium on barberry, a dicotyledonous plant, and the sporophytic phase of its mycelium on various cereals and grasses, monocotyledonous plants. This behavior of rusts is known as heteroecism. In other words, heteroecism is that phenomenon in which a rust-fungus requires two different kinds of hosts in order to complete its life-cycle and produce all the kinds of spore-forms which it is capable of producing.

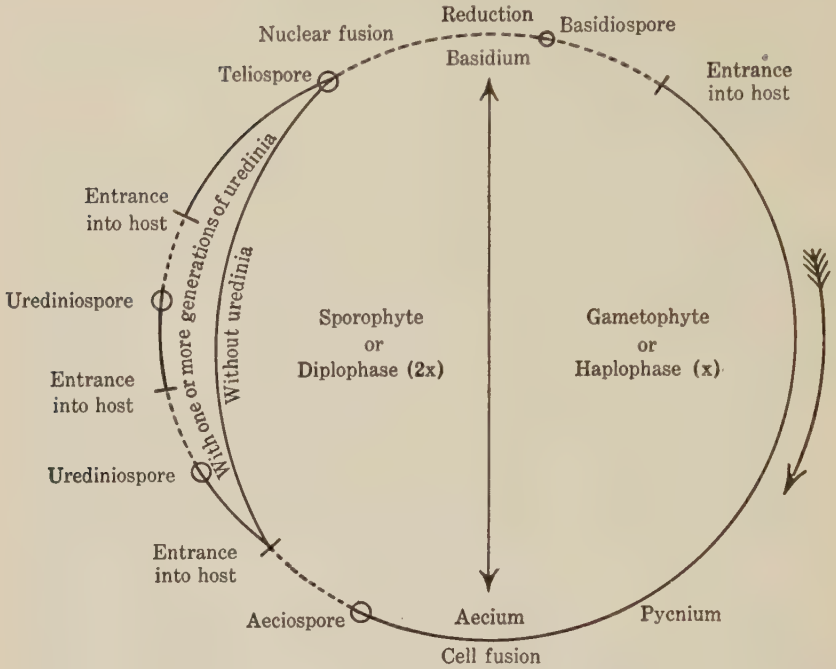

FIG. 3. — Diagram of the life-cycle of a macrocyclic rust: solid lines represent the course of vegetative development within the host, interrupted lines represent the course of development carried on by means of the spores. (Original.)

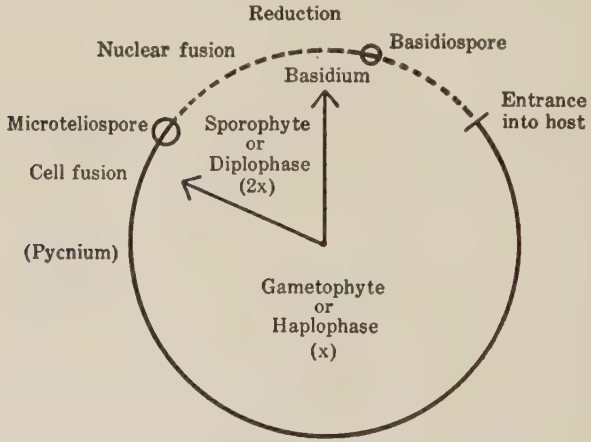

FIG. 4. — Diagram of the life-cycle of a microcyclic rust: solid lines represent the course of vegetative development within the host, interrupted lines represent the course of development carried on by means of the spores. (Original.)

THE SORUS AND ITS SPORES IN MACROCYCLIC SPECIES

Structure of the sorus. — The fruiting or reproductive structure of a rust is a sorus.[1] All sori possess essentially the same structural parts, but vary greatly as to the extent of their development. The sorus arises within the host (with very rare exceptions) from a small mass of closely intertwined hyphae, the primordium (Fig. 2). As the primordium develops it changes in well differentiated forms into an upper and lower part (Fig. 5). A layer of initial cells, the hymenium, is formed across the lower part from which the spores arise and accumulate in the upper part, where space has been made by disintegration. From the hymenium the spores are produced either singly or in chains. Often there are accessory parts, which serve the purpose of protection or as aids in discharging the spores. Such are the peridium and paraphyses. The mature sorus is a small definite structure, generally of characteristic appearance. It is usually covered at first by overlying host-tissue or by portions of the outer cell-wall, and is set free either by early rupture of the same or by weathering. When open to discharge spores, and no peridium is present, it is said to be naked.

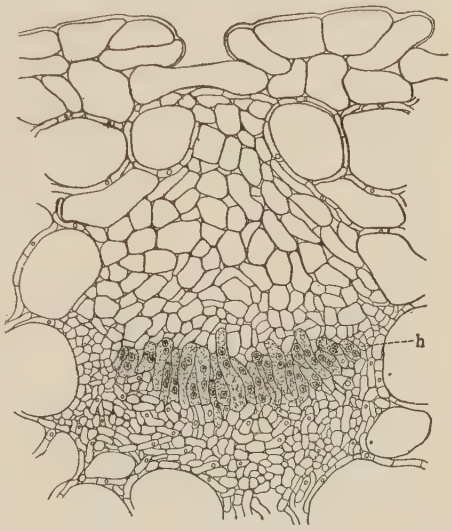

Fig. 5. — Early stage of a sorus, before the spores begin to form: aecium of *Uredinopsis mirabilis* beneath a stoma in the leaf of *Abies balsamea;* upper part of sorus filled with cells of the plectenchyma, which after a time disintegrate and make room for the spores; the middle layer of upright cells *h*, constitutes the hymenium. (After Adams, 1919.)

In consistency the mature sori may be powdery, from the successive falling away of the spores, or they may be compact and firm, or, in some species, soft and gelatinous. In color the various shades of yellow and reddish-brown predominate, but some rusts are so pale as to look white, while others are dark enough to appear black. The spore-structures are sometimes truly white although never truly black, but the aggrega-

[1] The term sorus is derived from the Greek σορός, a mortuary urn, or σωρός, a heap or pile, referring both to form and contents.

tion of very dark-brown spores may give the effect of a blackish sorus. In shape and size there is great variation among the sori (Fig. 6). Often they are roundish or oval, about two-tenths to one millimeter across and more or less cushion-shaped; some are cup-shaped, one-tenth to four-tenths millimeters or more across; others project as cylindric, filiform, columnar, or wedge-shaped masses varying in length from two or three millimeters up to ten or twenty millimeters or more.

The spores also vary greatly in size, shape, and number of cells. The color, thickness, and surface markings of the walls are also exceedingly variable. Some spores are borne singly or in fascicles on pedicels of varying length; others are sessile and either single or in chains.

Accessory parts. — The sorus often includes a peridium or paraphyses, and sometimes is surrounded by a more or less evident mycelial felting. A peridium (sometimes called pseudoperidium) is a well-defined tissue-like envelope, which usually projects beyond the surface of the plant (Fig. 7 *p*). Paraphyses, either peripheral, *i.e.*, around the margin (Fig. 8 *A*), or discal, *i.e.*, distributed among the spores (Fig. 8 *B*), are free sterile elements, usually extending to the surface of the plant or above it, or in subepidermal telial sori they may form a compact mass of sterile elements, usually brown, and variable in amount (Fig. 8 *C*). Both the peridium and paraphyses are derived from the hymenium, but about any sorus there may be in some cases, in addition to the sorus proper, a more or less definite mycelial felting (Fig. 7 *a*) originally derived from the same primordium as the sorus, which is sometimes called a pseudostroma.

Succession of sori. — Every macrocyclic species produces essential sori, and sometimes accessory sori, four kinds in all, which succeed one another in the life-cycle in the following order: pycnia, aecia, uredinia and telia (Figs. 6 and 9). Of these the aecia and telia are essential to the full development of a macrocyclic species, while the pycnia and uredinia are accessory kinds, and may or may not be produced.

The mycelium of the gametophytic phase first gives rise in typical species to very small sori called pycnia (Figs. 6 *p* and 9 *p*). They have also been called spermogonia, from the assumption that they are sexual structures. The pycnia produce pycniospores,[1] also called spermatia.

In addition to the pycnia there always arise from the same mycelium other and larger sori, which are called aecia (Figs. 6 *a* and 9 *a*), whatever their external form may be. Aeciospores are binucleate and germinate

[1] The word "pycnospore" is not a derivative of pycnium, and is not an accurate or consistent term for use in connection with the rusts.

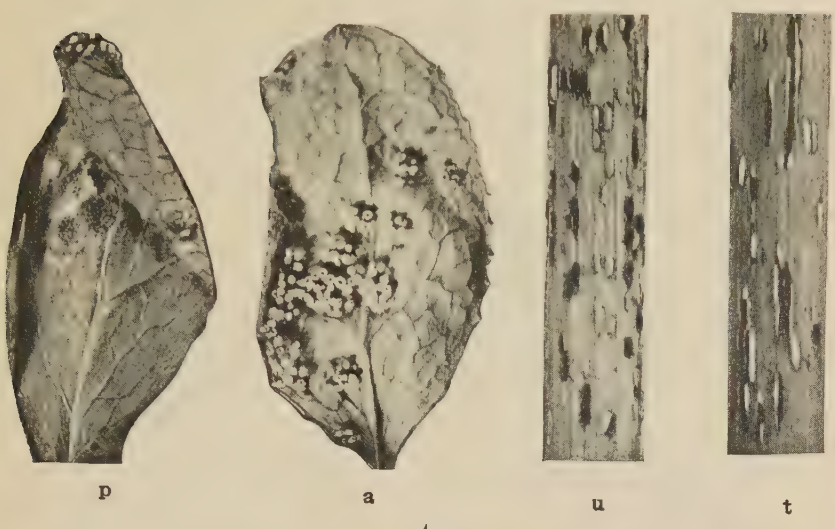

FIG. 6. — Different forms of sori belonging to the same species of rust: *A Puccinia graminis*, *p* pycnia on upper surface and *a* aecia on under surface of leaves of barberry (*Berberis vulgaris*), *u* uredinia and *t* telia on stems of wheat (*Triticum vulgare*), slightly magnified; *B* Gymnosporangium, *p* pycnia of *G. globosum* from leaf of Crataegus, *a* aecia of *G. corniculans* from leaf of Amelanchier, *t* telia of *G. clavariaeforme* on stem of Juniperus, before and after expansion by absorption of moisture. (*B a*, *t* after Kern, 1911; others original.)

(Fig. 10 *a*) by producing a hypha, usually called a germ-tube, which grows indefinitely and usually remains unseptated until it enters the host, generally through a stoma. It then ramifies into a much septated mycelium of binucleate cells.

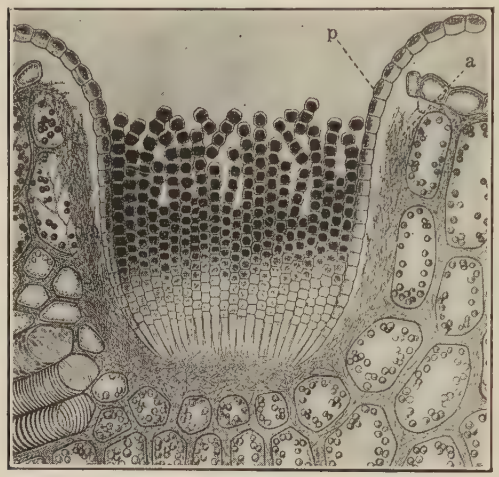

Fig. 7. — Aecium of *Puccinia graminis*, showing chains of aeciospores arising from the elongated cells of the hymenium, surrounded by the peridium *p*; *a* felting outside the aecium, the pseudostroma. (From an early diagrammatic drawing.)

The sporophytic phase, initiated by the aeciospore and continued by the resulting mycelium, produces in the majority of species a uredinium (Figs. 6 *u* and 9 *u*) as its first sorus. The uredinial stage is of a conidial or repeating nature, the urediniospores having the same function and sometimes the same form as the aeciospores. The urediniospore is binucleate. It germinates (Fig. 10 *u*) and infects the host in the same manner as an aeciospore. The resulting mycelium in some species and under favorable conditions may again produce uredinia, which in

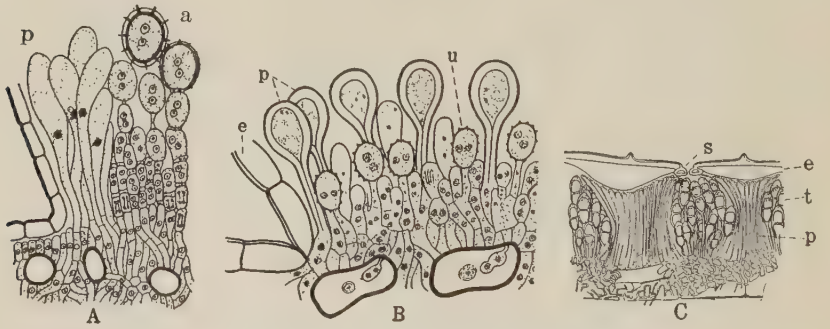

Fig. 8. — Paraphyses: *A* peripheral, at border of aecial sorus of *Phragmidium rubi*; *B* discal, in uredinium of *Melampsora helioscopiae*; *C* subepidermal, between telia of *Puccinia gladioli*, each sorus under a stoma; *p* paraphyses, *a* aeciospores in chains, *u* urediniospores forming between the paraphyses, *t* teliospores, *e* epidermis, *s* stoma. (*A* and *B* after Sappin-Trouffy, 1896; *C* after Dietel, 1897a.)

turn can repeat the process; but eventually telia (Fig. 6 *t* and 9 *t*) must be formed to complete the cycle.

Telia are the ultimate sori in the sporophytic phase. In general appearance both the telia and their teliospores are usually unlike aecia or uredinia and their spores. The teliospores germinate either by extruding a germ-tube, which is usually called a promycelium (Fig. 10 *t*) or in some genera, as Coleosporium, by internal division (Fig. 10 *c*).

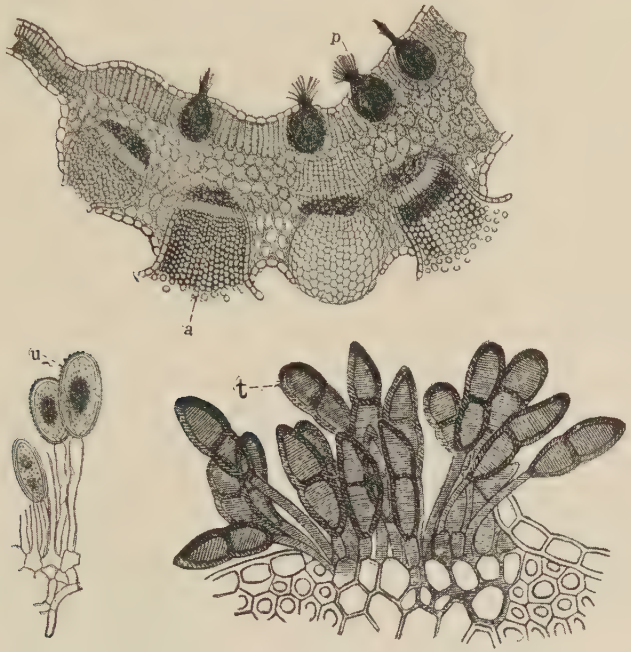

FIG. 9. — Succession of sori in the life-cycle of *Puccinia graminis*, a macrocyclic rust: section of barberry leaf with four pycnia *p* above and four aecia *a* below; telium *t* and part of uredinium *u* from wheat leaf. (After de Bary, 1887.)

The contents of the promycelium soon divide and form a basidium (Figs. 28 and 29 *A*), which in turn gives rise to four (rarely two) free basidiospores. Basidia and basidiospores are likewise formed when the contents of the spore are not extruded (Fig. 29 *B*, *C*).

Pycnia. — The pycnia[1] are borne on the gametophytic mycelium.

[1] Pycnium is derived from the Greek πυκνός, dense or compact. The term pycnidium, derived from the same root, has been used by some writers in this connection, but it seems best to confine its use to the similar but probably not homologous structure in ascomycetous fungi.

They are also known as spermogonia or spermogones. Both the pycnium and pycnial stage are represented by the numerical cipher 0.

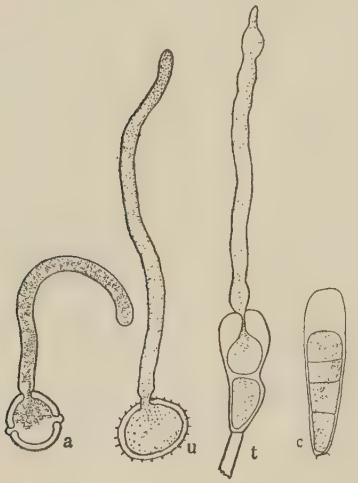

FIG. 10. — Germinating spores: *a* aeciospore and *u* urediniospore forming germ-tubes, which directly infect the host; *t* teliospore, whose germ-tube develops a basidium bearing basidiospores; *c* teliospore germinating without a germ-tube, the basidium of four cells being formed within the spore. (*a* after Dodge & Adams, Mycologia **9** : 27; *c* after Grove, 1913b; *u* and *t* original.)

Pycnia are subcuticular, subepidermal, or subcortical in origin. Subepidermal pycnia are globoid, flask-shaped, conoidal or hemispheric structures, walled in with numerous hypha-like paraphyses and filled with masses of pycniospores (Fig. 11 *c*), also called spermatia. In pycnia of this type there is a definite aperture or ostiole for the escape of the pycniospores. The projecting paraphyses, also designated as ostiolar filaments, may extend for variable lengths above the surface of the host. The pycnia in other cases, both subcuticular (Fig. 11 *a*) and subcortical (Fig. 11 *b*), are broad flat structures and open by slits or irregular rupture for the escape of the spores, which may be numerous above the flat hymenial layer. In such cases there are no paraphyses.

The pycniospores are abstricted successively from the ends of fertile hyphae, pycniosporophores, more

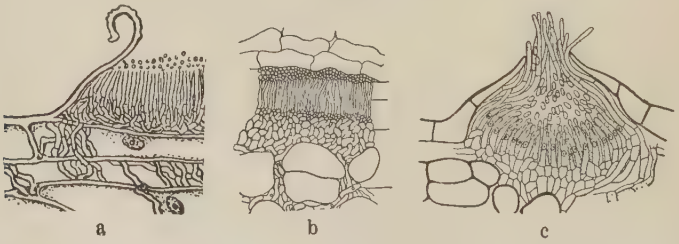

FIG. 11. — Pycnia: *a* subcuticular, of Pucciniastrum; *b* subcortical, of Cronartium; *c* subepidermal, of Gymnosporangium. (*a* after Klebahn, Zeits. Pflanzenkr. **13** : 152; *b* after Adams, 1919; *c* after Blackman, 1904.)

usually called spermatial hyphae (Fig. 12), which form the hymenial or basal lining of the pycnium. These spores are small, roundish or oval, thin-walled bodies, without surface markings, and contain a single rela-

tively large nucleus but not much protoplasmic or reserve substance (Fig. 12 *A*). They are capable in some instances apparently of slight germination but, so far as known, not of infection, and until recently were thought to have no demonstrable function. In connection with pycnial formation there is usually production of a sugary secretion or nectar, which, becoming partially dried, may hold the pycniospores together in an agglutinated mass. Sometimes the secretion is so abundant as to fall away in drops. It is attractive to insects, and it is said that in Japan children have a fondness for that which comes from the large pycnia on pine branches.

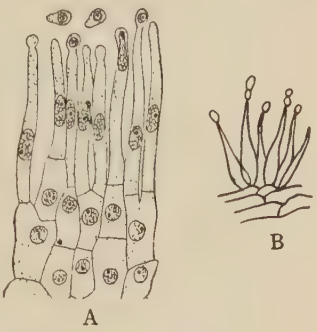

FIG. 12. — Pycniosporophores bearing pycniospores: *A* from *Cronartium ribicola* on Pinus, very greatly magnified, showing nuclei; *B* from *Puccinia graminis* on Berberis, much magnified. (*A* after Colley, 1918; *B* after de Bary, 1866b.)

Aecia. — The aecia[1] are the essential sori produced by the gametophytic mycelium in macrocyclic rusts. The structure and formation of the aecium are so varied in different species and genera that several other terms are in existence for some of the variations. The symbol for the aecium in all its forms and of the aecial stage is the Roman numeral I.

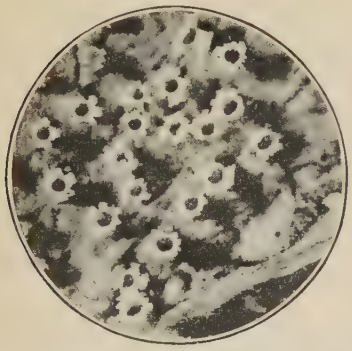

FIG. 13. — Cupulate aecia of *Puccinia grossulariae* on *Ribes floridum*, showing the torn and recurved border. (Photograph by Holway.)

There are six well-marked forms of aecia that are distinguishable by their general external appearance: cupulate, cornute, operculate, naked, stylosporic and hyphoid.

The cupulate form of aecium, generally known as the cluster-cup or aecidium, is doubtless the one most commonly thought of in this connection (Fig. 13). Here each aecium is provided with a peridium, consisting of a single layer of cells, which opens out into a cup-like or nearly cylindric receptacle with a more or less jagged and recurved border, enclosing a mass of spores (Fig. 7). When borne in

[1] Aecium is from the Greek *αικία*, a wound, referring to the rupture of the epidermis; or possibly from *οἶκος*, a house or apartment.

groups (Fig. 6 *Aa*) the designation cluster-cup is especially appropriate. This is the cupulate or aecidioid aecium (from the form-genus *Aecidium*).

In other forms of aecia the peridium may become horn-like (Fig. 14), thin at the sides but with apex somewhat pointed and thickened, usually rupturing by longitudinal slits, and made up of characteristically marked and imbricated cells (Fig. 15). These are the cornute or roestelioid aecia (from the form-genus *Roestelia*), especially so recognized if occurring on pomaceous hosts.

Fig. 14. — Cornute aecia of *Gymnosporangium cornutum*, showing *a* the horn-like form and *b* the lateral rupture when more mature. (*a* after Ørsted, Bull. Acad. Sci. Copenhague **1866** : pl. 4; *b* after Kern, 1911.)

Other aecia having a blister-like (Fig. 16 *a*), tongue-shaped (Fig. 16 *b*), or cylindric (Fig. 16 *c*) peridium, which is often more than one cell-layer in thickness above (Fig. 17), and usually is in form of an operculum, may be said to be operculate or peridermioid (from the form-genus *Peridermium*). Such aecia occur on coniferous hosts, and are most characteristically developed when on woody stems or trunks.

Still other aecia may be surrounded by paraphyses instead of peridia; and still others may be without either, and are then less delimited in form than most kinds; both of these are naked or caeomoid aecia (from the form-genus *Caeoma*). All of the foregoing aecial forms have the aeciospores in chains, and often have noticeable intercalary cells between the spores.

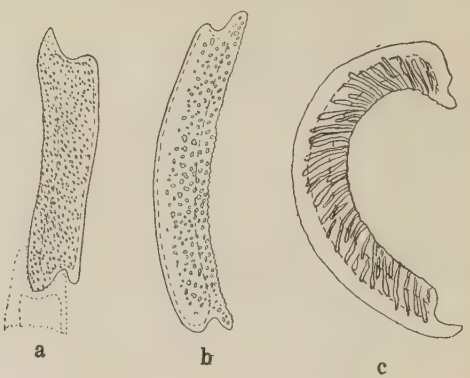

Fig. 15. — Peridial cells of cornute aecia: *a Gymnosporangium cornutum* on Sorbus, *b G. clavariaeforme* on Amelanchier, *c G. juniperi-virginianae* on Malus. (After Kern, 1911.)

Less easily recognized as aecia, with spores borne singly on pedicels

and usually without peridia or paraphyses, are the stylosporic or uredinoid aecia (from the form-genus *Uredo*). These stylosporic aecia have

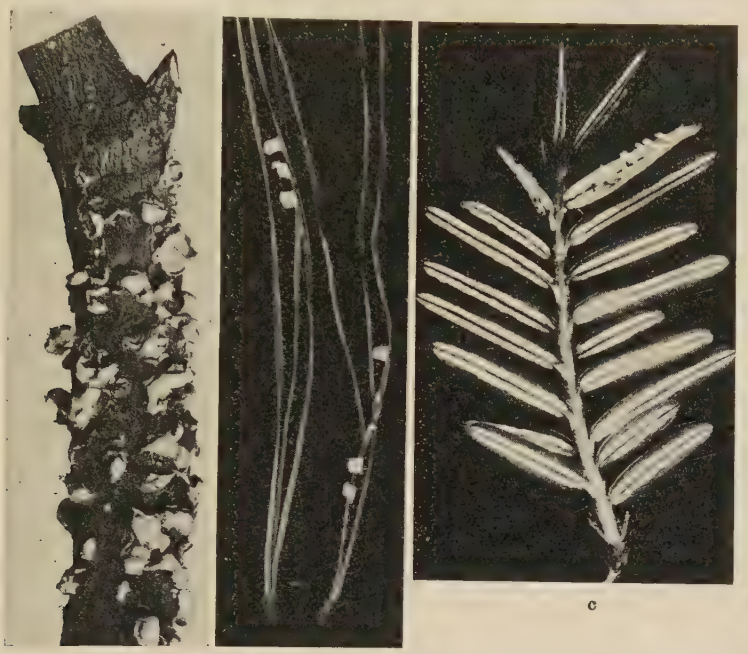

FIG. 16. — Operculate aecia: *a* blister-like, from *Cronartium ribicola* on Pinus, characteristic form showing the operculum (peridium) ruptured at the sides and raised from many of the sori; *b* tongue-shaped, from *Coleosporium carneum* on Pinus; *c* cylindric, from *Pucciniastrum hydrangiae* on Tsuga. (*a* and *c* after Adams, 1919; *b* original.)

been and still are often referred to as "primary uredo," because of their general resemblance to well-known forms of uredinia. The place of these sori in the life-cycle of the species in which they occur, together with their mode of origin, mark them, however, as true aecial stages. To indicate this difference when a symbol is used, it may be written I^{ii}, to be read, stylosporic or uredinoid aecia.

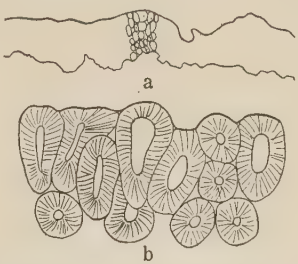

FIG. 17. — Section of peridium of *Cronartium harknessii* on *Pinus contorta:* *a* middle portion with a few cells drawn in place, *b* a part more magnified. (Original.)

The term "primary uredo" is also applied occasionally to the true uredinia which arise from aeciosporic infection, while the uredinia from urediniosporic infection are distinguished as "secondary uredo."

There is still another form of aecium, at present known only in the genus Dasyspora, which has colorless, branching hyphae extending mold-like above the epidermis, each branch terminated by a single colorless spore (Figs. 18 and 86). From its appearance it may be characterized as hyphoid.

Fig. 18. — Hyphoid aecia, surface view, somewhat magnified. (Original.)

Aeciospores (Fig. 19) are always one-celled. The walls of aeciospores are verrucose, except in the species with stylosporic aecia and in the genus *Olivea*, where they are echinulate. The walls are usually light colored, yellowish, or colorless but in certain cases (*e.g.*, in some of the cedar rusts, *Gymnosporangium*), they are of varying shades of yellowish-brown. Pores may or may not be evident. The protoplasmic contents of the aeciospores are usually granular, liberally supplied with drops of oil and other food substances, and are generally of an orange color when fresh, although they may sometimes be yellow or colorless.

Uredinia. — In most species the first sori to arise from the sporophytic mycelium, and consequently those immediately succeeding the aecia are the uredinia.[1] The uredinia may be naked, either with or without paraphyses, or in some species surrounded by peridia (Fig. 20). In some cases the peridia may be well developed with a specially formed ostiole having well differentiated ostiolar cells (Fig. 21). Naked uredinial sori with powdery reddish-yellow spores are sufficiently noticeable and common

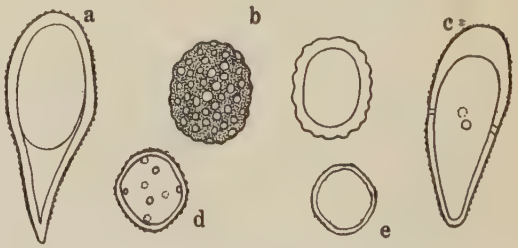

Fig. 19. — Various forms of aeciospores: *a Cronartium pyriforme* on Pinus sp., *b Melampsora pyrolae* on *Picea rubra*, surface and section view, *c Ravenelia ingae* on *Inga edulis*, *d Gymnosporangium globosum* on *Crataegus mollis*, *e Puccinia violae* on *Viola canadensis*. (Original.)

[1] Uredinium is from the Latin word *uredo*, a blight or blast, which in turn is from *urere*, to burn.

so that they tend to dominate the popular conception of rusts. It is the rusty appearance, like rusted iron, which is responsible for the common name *rust* and the Latin name *uredo*, and even the name of the order, Uredinales. The symbol for the uredinium and the uredinial stage is the Roman numeral II.

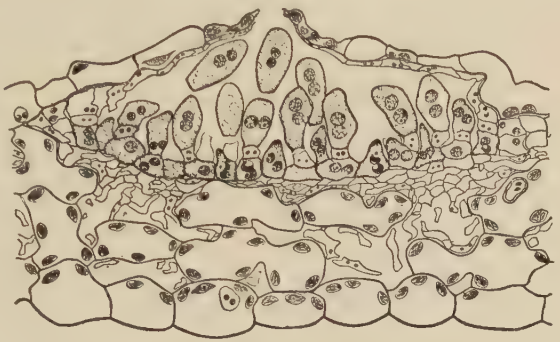

FIG. 20. — Uredinium of *Hyalopsora polypodii* with young urediniospores: a slender, largely collapsed peridium lies beneath the epidermis. (After Moss, 1926.)

Functionally the urediniospores are repeating spores, and therefore of a conidial nature, having the possibility of reproducing the uredinial stage over and over indefinitely. When present they are the stage usually responsible for the rapid spread of the rust. They usually germinate without a resting period, and consequently are often called "summer" spores.

Urediniospores (Fig. 22) may be borne singly on pedicels from which they readily separate, or in chains (Fig. 23 *u*), and are single-celled. The walls of the spores are usually colored, yellowish or brownish, and with few exceptions are roughened, being either echinulate or verrucose. There is great variation in shape and size, and in the thickness of the walls.

FIG. 21. — Upper part of peridium of a uredinium of *Pucciniastrum arcticum* on Rubus: *p* peridium; *e* epidermis. (After Moss, 1926.)

Germ-pores (Fig. 22) are frequently evident, and their number and location are often important diagnostic characters for identification purposes. In some species there is a definite number of pores, which are located in zones at, above or below the equator, near the apex, or near the base. In other species there is an indefinite number, apparently more or less indiscriminately scattered over the spore. Pedicellate urediniospores are as a rule easily detached from their pedicels, leaving a scar or hilum.

In general, the uredinia differ from the aecia in structure both of sori and spores. There are cases, however, where the uredinia are of a similar structure to the aecia which precede them, as in *Puccinia ambigua* or *Uromyces scrophulariae*. The instances like these where aecia of the common, cupulate form are followed by uredinia of the same form are rather rare. Uredinia of this sort, because of their resemblance to the aecia which precede them, are best called aecidioid, but usually have been referred to as "secondary aecidia," being like aecia in appearance, but unaccompanied by pycnia and borne on sporophytic mycelium. They may be conveniently distinguished from the ordinary uredinia by the symbol II^i, to be read, aecidioid uredinia.

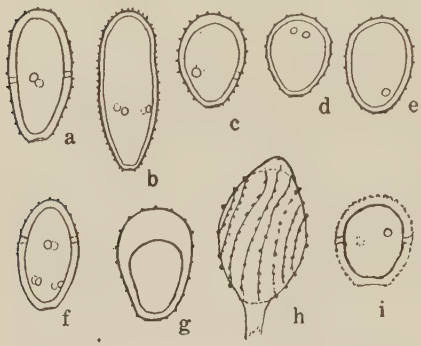

FIG. 22. — Various forms of urediniospores: *a Puccinia graminis* on *Sporobolus cryptandrus*, *b Ravenelia leucaenae*, *c Ravenelia ingae*, *d Puccinia asterum* on Carex, *e Puccinia grossulariae* on Carex, *f Ravenelia versatilis* on Acacia, *g Puccinia fraxinata* on Fraxinus, *h Pileolaria toxicodendri* on Rhus, *i Puccinia ellisiana* on Andropogon; *c* and *g* with wall thicker above, *a* and *i* with four pores and *c* with three pores in the equator, *b* with four pores below the equator, *d* with two pores much above the equator, *e* with one pore near the hilum, *f* with eight pores in two zones, *g* with pores indistinct, *a–g* echinulate, *h* and *i* verrucose. Uniformly magnified about 400 diameters. (Original.)

Germination of urediniospores ordinarily takes place at their maturity, if conditions are favorable, but the capacity for germination may be retained for a considerable time under some environmental conditions.

In some species there occur specially developed urediniospores (Fig. 24) with thicker and sometimes more highly colored walls, which act as resting spores and are known as amphispores.[1] Although clearly belonging to the repeating stage, amphispores (*e.g.*, in *Puccinia vexans* and

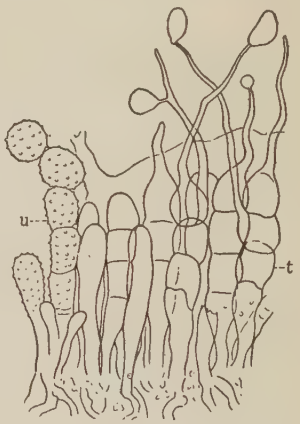

FIG. 23.— Urediniospores and teliospores in same sorus of *Coleosporium rhinanthacearum*: *u* urediniospores in chains, *t* teliospores in process of germination. (After Tulasne, 1854b.)

[1] The term amphispore, from the Greek *αμφί*, both or between, and *σπορά*, spore.

Uredinopsis spp.) may differ from the urediniospores of the same species in color of contents, shape, markings and thickness of wall, pore arrangements, and in the possession of persistent pedicels; and yet they give rise to a mycelium that bears urediniospores of the usual character. The sori may be distinguished from the ordinary uredinia by the symbol II^{x}, to be read, amphisporic uredinia.

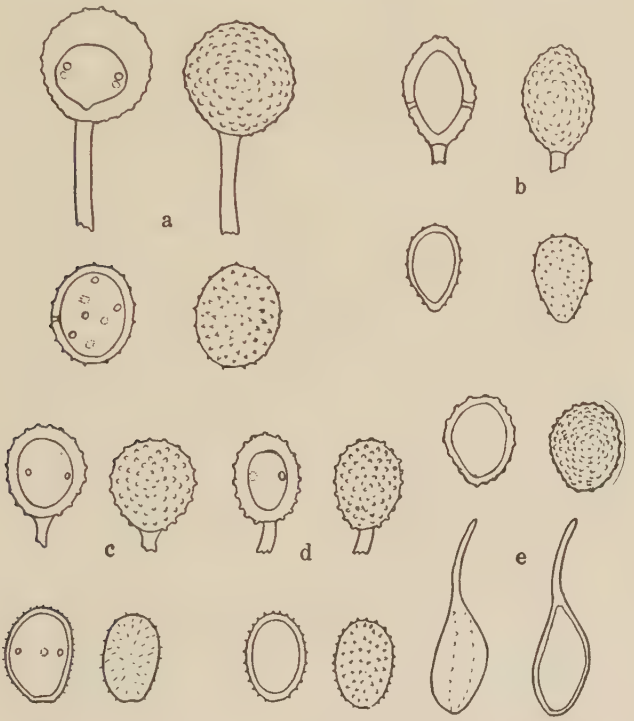

Fig. 24. — Amphispores and ordinary urediniospores of the same species, shown both in surface view and in section: *a Puccinia vexans* on Bouteloua, *b P. caricis-strictae* on Carex, *c P. atrofusca* on Carex, *d Uromyces rottboelliae* on Rottboellia, *e Uredinopsis copelandi* on Asplenium: the two upper spores of each group of four are amphispores, all of which are verrucose, while the lower of each group are the ordinary urediniospores, and all echinulate. Uniformly magnified about 400 diameters. (Original.)

Eventually in the ordinary course of events, conditions being favorable to continued growth, every sporophytic mycelium will follow its uredinial stage by the production of telia. Teliospores may at first arise in the uredinia (Fig. 23), and gradually replace the urediniospores in the sorus. In some species, however, and under certain conditions,

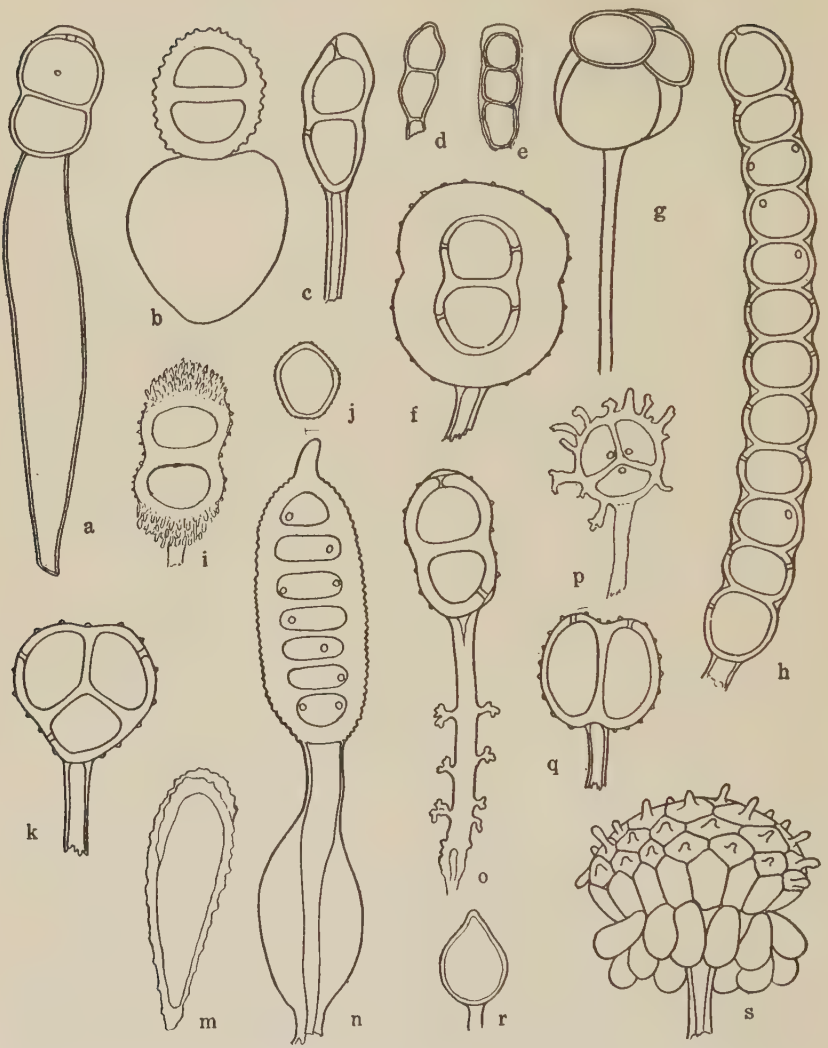

FIG. 25. — Various forms of free or fascicled teliospores, family Pucciniaceae: *a Puccinia elatipes* on *Lippia myriocephala*, *b P. globosipes* on *Lycium andersonii*, *c P. graminis* on *Sporobolus cryptandrus*, *d P. oxalidis* on Oxalis, *e P. phakopsoroides* on *Olyra latifolia*, *f Uropyxis amorphae* on *Amorpha fruticosa*, *g Cystomyces costaricensis* on unknown leguminous host, *h Xenodochus carbonarius* on *Sanguisorba officinalis*, *i Dasyspora faveolata* on *Xylopus granidflora*, *j Endophyllum decoloratum* on Wedelia, *k Triphragmium ulmariae* on *Filipendula rubra*, *m Ctenoderma cristatum* on Cupania, *n Phragmidium disciflorum* on *Rosa bengolensis*, *o Prospodium appendiculatum* on *Stenolobium molle*, *p Nyssopsora clavellosa* on *Aralia nudicaulis*, *q Diorchidium woodii* on *Milletia caffra*, *r Botryorhiza hippocrateae* on *H. volubilis*, *s Ravenelia spinulosa* on *Cassia holwayana*. Uniformly magnified about 400 diameters. (*g* after Dietel, Ann. Myc., **24** : 291; all others original.)

particularly in the tropics, the appearance of telia may not take place with regularity, or only after very long intervals.

Telia. — Of the four sorts of spores borne in sori the teliospore is commonly the one most readily recognized and the one on which most stress has been laid in systematic treatises. Such spores are borne in a

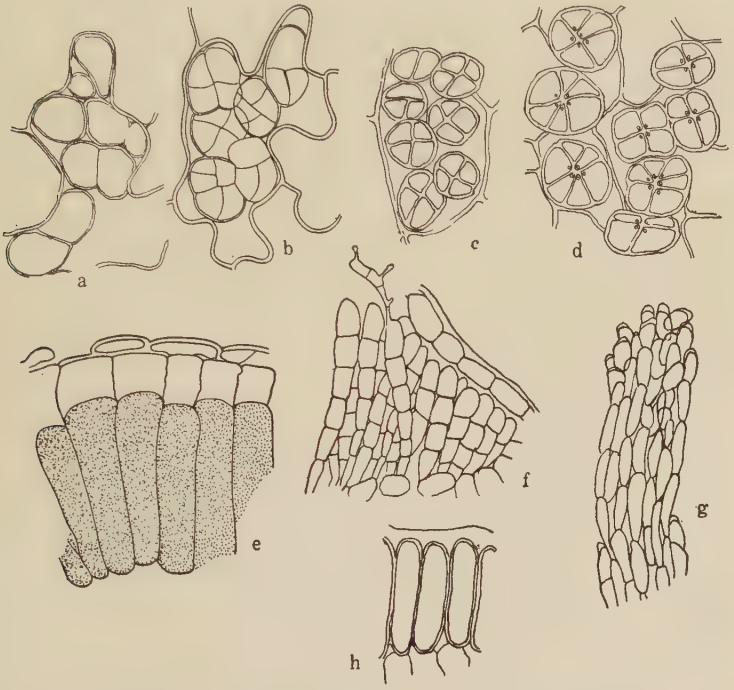

FIG. 26. — Various forms of compacted teliospores, family Melampsoraceae: *a Melampsorella elatina* on *Stellaria nemorum*, *b Hyalopsora aspidiotus* on *Phegopteris dryopteris*, *c Uredinopsis osmundae* on *Osmunda claytoniana*, *d Pucciniastrum sparsum* on *Arctostaphylos alpina*, *e Coleosporium melampyri* on *Melampyrum sylvaticum*, *f Melampsoropsis rhododendri* on Rhododendron, *g Cronartium asclepiadeum*, *h Melampsora larici-pentandrae* on Salix; *a–d* in vertical view from surface of host, *e–h* in sectional side view. (*a*, *b*, *d*, *e*, *g*, after Fischer, 1904; *h* after Klebahn, Zeits. Pflanzenkr. **7** : 331; *f* after de Bary, Bot. Zeit., 1879; *c* original.)

sorus designated as the *telium*.[1] Other terms are teleutospore and teleutosorus, but for the stage or phase to which they belong no satisfactory adjective exists in the older terminology. This telial stage as well as its sorus is represented by the Roman numeral III as a symbol.

The telia vary so greatly in the different genera that it is difficult to give any general characterization. In many forms the telia have more

[1] The term is derived from the Greek τελειος or τελεος, complete or perfect.

of a tendency toward compactness than in the other kinds of sori, although in some forms they are quite the opposite, being either pulverulent or of a gelatinous nature. Telia may be waxy layers, more or less definite crusts or columns, or erumpent, exposed, cushion-like masses. In a few cases teliospores are borne singly within the tissues, as occurs to some extent in Uredinopsis, and in some tropical genera they are from the first exserted and more or less exposed above the epidermis. In other cases the telia remain buried under the epidermis for long periods, presenting a very different aspect from exposed sori.

The teliospores may be one- to several-celled, free, fascicled (Fig. 25), or compacted into layers (Fig. 26), and in either case may be borne singly or in chains (catenulate). The walls may be smooth or roughened, sometimes spinulose, but very rarely if ever genuinely echinulate. Sometimes the walls are distinctly laminate, with a firm, colored, inner layer and an outer, gelatinous, translucent layer, overlaid by cuticle (Fig. 25 *f*). In the walls of many teliospores there are more or less evident spots, or germ-pores, through which the germ-tube passes upon germination of the spore (Fig. 25 *c*, *h*, *k*, *o*, *p*, *q*). The number and arrangement of these pores in a teliospore-cell, if evident, is fairly constant for a species, but there are great differences between different species and genera.

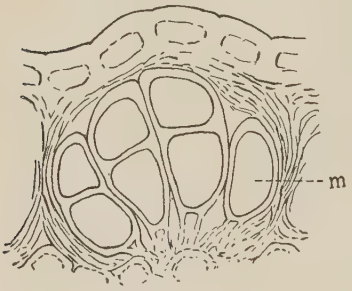

Fig. 27. — Small sorus of *Puccinia montanensis* showing one mesospore *m*, and three teliospores of the usual form. (Original.)

In some rusts having free two-celled teliospores, there are produced both two-celled and one-celled spores. The term mesospore has been applied to such one-celled spores (Fig. 27 *m*), although the term is occasionally used for the middle layer in the wall of a spore, when three layers can be distinguished. In some species such one-celled spores are few and occasional, but in others (*e.g.*, *Puccinia heterospora*) they are abundant (Fig. 51).

In many species the teliospores act as "resting" spores, germinating only after a longer or shorter period of dormancy. Frequently this condition coincides with the winter season and results in tiding the fungus over a period unfavorable for growth, due to which they have received the name of "winter" spores. In other species the teliospores are designated as "active," being able to germinate upon maturity, or so soon thereafter as to require no perceptible resting period.

THE SORUS AND ITS SPORES IN MICROCYCLIC SPECIES

The microcyclic, or short-cycle, rusts have only one mycelial body, which in general is of like nature and position in the life-cycle to that of the gametophytic mycelium in the macrocyclic rusts. No mycelium is produced in the sporophytic phase of a microcyclic rust.

Pycnia. — The microcyclic mycelium may or may not bear pycnia. Such pycnia are of the same nature and structure as those of macrocyclic rusts, previously described.

Microtelia. — In addition to the pycnium only one form of sorus is found in microcyclic rusts. This sorus in its early stages proceeds to develop like an aecium. It takes on later either the form of an aecium or else that of a telium, according to the species. In all cases, however, the spores at maturity germinate like true teliospores (Figs. 28 and 29). Due to this double nature, in which the sorus starts as if it were to produce aeciospores, but ends by producing spores that resemble either aeciospores or teliospores, the name "aeciotelium" has been suggested, but *microtelium* is a better term for such a sorus, indicating its relation to the microcyclic stage, and will be employed in this work. However, in gross morphologic structure the sorus with its spores simulates either an aecium, *e.g.*, Endophyllum, or a telium *e.g.*, Polythelis, and for many purposes, especially in systematic treatises, it is more convenient to use the shorter words, aecium and telium, respectively, than the longer word, microtelium.

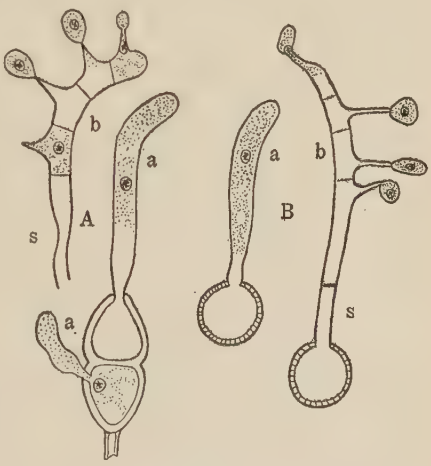

FIG. 28. — Germination of microteliospores, *a* promycelium, *b* basidium with basidiospores, *s* stalk: *A Puccinia malvacearum; B Endophyllum sempervivi.* (*A* after Sappin-Trouffy, 1896; *B* after M. & Mme. Moreau, 1919.)

When microteliospores germinate immediately upon maturity, the term lepto-form is often applied, but when a period of rest is required before germination takes place, the term micro-form is used. The same designations are also used in connection with generic names, thus there are species of *Lepto-Puccinia*, *Lepto-Uromyces*, etc. The detailed development of microcyclic sori is given in a later chapter.

THE BASIDIUM AND BASIDIOSPORES

Upon germination of the teliospore or microteliospore a short germ-tube, the promycelium, is usually formed, the contents of which, generally collected at the distal end, are converted into a four-celled (or rarely a two-celled) basidium (Figs. 28 and 29 *A*), for which the proximal end of the promycelium often serves as a stalk (Figs. 28 *s* and 29 *s*). In some genera no evident promycelium is produced, *e.g.*, Coleosporium (Fig. 10 *c*), Chrysopsora (Fig. 29 *B*), Ochropsora (Fig. 29 *C*), and Goplana (Fig. 100), the basidium being formed while within the spore-cell. The basidium gives rise to four (in some species two) stalked or sessile basidiospores, also called sporidia, usually in basipetal order (Fig. 29), which are small, roundish or oval, kidney-shaped or spindle-shaped, thin-walled bodies and generally without surface sculpturing (Fig. 29 *b*). These spores may germinate at once and by means of a very short and slender tube (Fig. 30) or beak (Fig. 131) infect the host by penetrating the cuticle or rarely by entering a stoma. No sorus is formed in connection with the basidiospores.

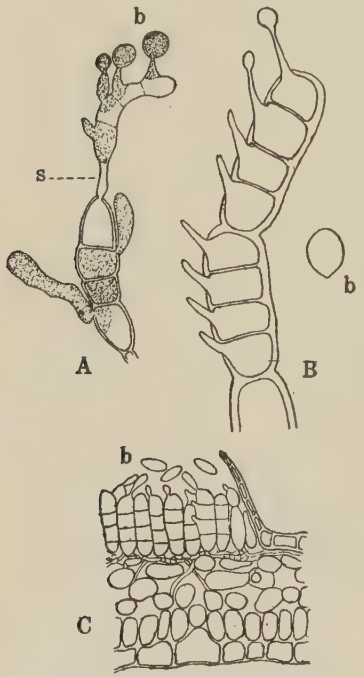

FIG. 29. — Germination of teliospores, *A* with basidium external, supported on the stalk *s*, *B* and *C* with basidium internal, basidiospores developing in basipetal order, *b*, *b*, *b* forms of basidiospores: *A* Gymnosporangium, *B* Chrysopsora, *C* Ochropsora. (*A* after Kern, 1913; *B*, *C* after Dietel, 1897a.)

FIG. 30. — Basidiospore of *Uromyces fabae* in germination penetrates the outer wall of the epidermis of *Vicia fabae*, and forms a hypha beneath. (After de Bary, 1863a.)

LIFE-CYCLES ILLUSTRATED

The attempt has been made in the foregoing discussion to give as full and comprehensive and yet as concise an idea of the rusts and of their transformations and terminology as the intricate nature of the

subject will permit. It may now be well to illustrate further the variations in life-cycles with some specific examples drawn from common forms of the north temperate zone.

Macrocyclic rusts. — Rusts which usually produce the full number of spore-stages, pycnia, aecia, uredinia and telia, may be divided into two groups: (a) those possessing uredinia unlike the aecia in appearance, and (b) those with uredinia similar to the aecia. In both groups the uredinia are not infrequently partly or wholly absent, due to hereditary influence or to unfavorable conditions for development.

(*a*) *Uredinia unlike aecia.* — The very common stem rust of wheat, *Puccinia graminis*, may be taken as an example of the first group in which uredinia are abundantly developed. This rust is heteroecious, as are nearly all of the grass and sedge rusts, and has the common cupulate form of aecia. The flask-shaped pycnia appear on the upper surface of barberry leaves in the spring. They are followed by aecia opposite them on the lower surface. Aeciosporic infection will not take place on barberry, but on wheat or a similar host it gives rise in a week or so to reddish powdery uredinia followed sooner or later by blackish compact telia with teliospores of the two-celled, free type. *Puccinia caricis*, with aecia on common nettles (Urtica) and uredinia and telia on various species of Carex, is a similar rust. As examples of other rusts belonging to the group, but which are autoecious may be mentioned *Puccinia convolvuli*, common on *Convolvulus sepium* and other kinds of morning-glory and *P. menthae* on various mints. In these autoecious species the spore-forms follow one another on the same host.

A rust which does not produce uredinia but otherwise is similar to the preceding is *Puccinia claytoniata* on the spring beauty. Especially well known in America is the common cedar rust, *Gymnosporangium juniperi-virginianae*, which is a typical example of a large number of species wholly lacking the uredinial stage, but from their structure and host relations clearly belonging to the first group. The latter differs from the examples previously cited in having cornute, *i.e.*, roestelioid aecia. It is heteroecious, the pycnia and the aecia occurring on the apple, with the telia of elongated, gelatinous masses, protruding from galls on the red cedar. In this rust the fungus is tided over winter in the mycelial condition in the gall, the teliospores being produced in the spring and germinating at maturity. Pycnia and aecia follow in early summer on the apple, and infection of the cedar takes place later in the season, usually developing slowly. *Gymnosporangium clavariaeforme*,

common in both Europe and America on hawthorn and juniper, is a similar rust.

A species of the first group having operculate, *i.e.*, peridermioid aecia, and with abundance of uredinia, is the very common American rust on asters and golden-rods, *Coleosporium solidaginis*. The pycnia and tongue-shaped aecia are on leaves of pine, while the uredinia and telia appear in great abundance on various genera of the Aster tribe. Other similar species of Coleosporium, found in various parts of the world, are *C. campanulae* and *C. senecionis*. The bark forms of operculate aecia have much thicker and stronger opercula than those of leaf forms, the exposed part of the peridium generally falling away in flakes. Of these *Cronartium ribicola* is a good example. Its pycnia and aecia form under the bark of five-leaved pines, even on the large trunks, and the uredinia and telia appear on currants and gooseberries.

The common world-wide rust of cultivated roses, *Phragmidium disciflorum*, is also a member of the first group. In this species, however, the aecia are naked, *i.e.*, caeomoid, but with somewhat rudimentary and inconspicuous paraphyses. The uredinia, which have conspicuous paraphyses, are abundant on the same host, and are followed by the large blackish telia. *Earlea speciosa* (*Phragmidium speciosum*) is a similar American rust of roses, but without uredinia.

(*b*) *Uredinia resembling aecia.* — An example of the second and much less common group of macrocyclic rusts, in which the uredinia are similar to the common form of aecia (aecidioid) in appearance, is that of *Puccinia ambigua* on the common cleavers, *Galium aparine*. This species is autoecious and in its uredinial condition possesses sori that do not differ in external appearance from the aecia, but are not accompanied by pycnia. They are borne on the sporophytic mycelium, but usually are not distinguished from the aecia. Another example of the second group, also an autoecious rust, but differing greatly in structure and habit from the preceding, is *Frommea obtusa* (also cited as *Phragmidium potentillae-canadensis*), on the common cinquefoil, *Potentilla canadensis*. Here the aecia (often called "primary uredo") closely surround the pycnia on the upper side of the leaf. They are somewhat waxy, while the true uredinia are scattered and pulverulent and chiefly on the under side of the leaf. The telia are blackish, pulvinate, velvety, with teliospores that are free and three- to five-celled. *Puccinia hieracii* is another example of this group in which the stylosporic aecia, *i.e.*, the so-called "primary uredo," differ but slightly in appearance from the true uredinia.

Microcyclic rusts. — In these forms, which are numerous, the mycelium, always of basidiosporic origin, may normally produce pycnia, followed shortly by microtelia. In the majority of cases, however, there are no pycnia. A good example of a microcyclic form is the common rust, *Puccinia arenariae*, on chickweeds (Stellaria, Cerastium, etc.). The telia are pulvinate, the teliospores two-celled, pedicellate and free. Another form of a microcyclic rust is that on various species of Aster, *Puccinia asteris*. And still another example is the more common *Puccinia malvacearum* on various mallows. In these three species pycnia are unknown and probably not formed, and the microtelia are markedly pulvinate, compact and aggregate, having a somewhat different aspect from the telia of most macrocyclic species.

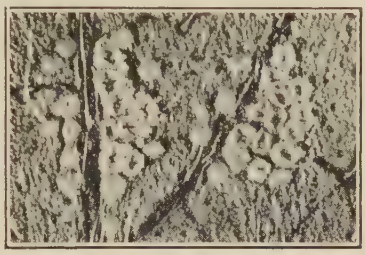

Fig. 31. — Surface view of two groups of sori of *Endophyllum decoloratum* on leaf of Wedelia. Magn. 7 diam. (After Olive & Whetzel, Am. Jour. Bot. **4** : pl. 3.)

Of the few species of microcyclic rusts having sori appearing like aecidioid aecia, *Endophyllum sempervivi* or any other species belonging to the same genus (Fig. 31), may be cited, while species of the tropical genus Maravalia (Fig. 32) are colorless, and have the general appearance of hyphoid aecia. Such species as these are sometimes accompanied by pycnia.

Fig. 32. — Surface view of groups of sori of *Maravalia pallida* on leaf of *Pithecolobium latifolium*, native of Trinidad. (After Arthur, 1922b, photograph by Thaxter.)

Mutable species. — A few species of rusts have been carefully studied, and others are known, which pass readily at times from the long-cycle to a condition that actually is, or else resembles a short-cycle condition. These are mostly species without a uredinial stage, or with uredinia resembling the aecia. Such species under conditions not fully determined will sometimes omit the aecia, or both aecia and uredinia, leaving only pycnia and telia, or possibly only the latter in the cycle.

The best known example of what appears to be the transition of a long-cycle to a short-cycle condition is found in *Gymnoconia interstitialis*, the orange rust on blackberries, the microcyclic form of the latter being called *Kunkelia nitens* (sometimes *Caeoma nitens*). An instance which simulates such a change is found in *Puccinia podophylli*, when the mycelium arising from basidiospores forms teliospores directly, particularly on basal sheaths of the host or on stems at surface of ground. In both rusts no uredinia are present during either the full or the abbreviated cycle. In the latter instance, however, it has been found that the teliospores give rise to a mycelium in the next generation that returns to the normal order of aecial and telial production.

An example of what appears to be a mutable species, having the aecia of similar appearance to the uredinia, is a tropical species, *Uromyces bidenticola*, on various species of Bidens, the microcyclic form being *Uromyces bidentis*. Some species, *e.g.*, *Uromyces acetosae*, which usually produce both aecia and telia, especially at the beginning of the season of growth, will later form only telia. These, and other species that could be named having a variable and uncertain behavior in the succession of their spore forms, are much in need of critical study.

RUSTS IN RELATION TO OTHER FUNGI

The rusts together with the smuts have been classed by many as a distinctive division of the Basidiomycetes called the lower Basidiomycetes. Both the rusts and smuts are predominantly parasitic, and differ in this regard from most of the higher Basidiomycetes which are chiefly saprophytic. The smuts, however, have been developed on artificial media, but not the rusts. A later and more natural arrangement divides the Basidiomycetes into three groups or sub-classes, (1) Hemibasidii: Ustilaginales (smuts); (2) Protobasidii: Uredinales (rusts), Auriculariales (Jew's-ear, etc.), Tremellales (gelatinous fungi); (3) Autobasidii (the remaining orders, mushrooms, polypores, puffballs, etc.). The Auriculariales and Tremellales show their relationship to the rusts by structural similarities, but their largely saprophytic habit associates them with the orders of the Autobasidii. With their basidia divided crosswise, *i.e.*, transversely septate, the Auriculariales in particular indicate relationship to the rusts. The interrelationship of the various orders of the Basidiomycetes, especially of the lower ones, is not clearly known, and the relations of the entire class to other groups of fungi are still more uncertain, although there are evident analogies with some of the Ascomycetes, as pointed out by de Bary nearly fifty years ago.

IMPORTANCE OF THE GROUP

Although mostly inconspicuous fungi the rusts are of unusual scientific interest because of the large array of forms, their varied spore-structures, and in many species the striking change of hosts (heteroecism). From a general standpoint they are of interest because of the injury and economic losses they cause in many plants. Most of our crop, forest and ornamental plants are subject to the ravages of these fungi. Wheat, oats and rye among the cereals; apples, pears and quinces among the fruits; beans, beets and asparagus among the vegetables; pines, cedars and willows among the trees; clover and timothy among the forage crops; and roses, hollyhocks and carnations among the ornamentals are some of the plants of economic importance that are affected. The practical extinction of the white pine forest in Norway has been brought about by the blister rust, and a similar fate is threatened in America. In a single season wheat rust may cause a loss in the United States of 200,000,000 bushels. In Germany in 1891, which was a "rust year," the loss on wheat and rye amounted to fully GM170,000,000 ($42,500,000). The loss from wheat rust in Australia sometimes amounts to £3,000,000 ($15,000,000) in a single season. Eriksson has estimated that taking all grain-growing countries together the average annual loss from rust amounts to over $300,000,000. It is a matter of history that the ancients were aware of the losses to their crops from these fungi.

On account of the great variation of form and habit in the different species of rusts, many of which have never been investigated, it is impossible to make an accurate estimate of the size of the group. It is probable that there are about three or four thousand valid species known, of which a little more than one-third are reported from North America. The number of species or genera is largely dependent upon the concepts held by those engaged in taxonomic work. Perhaps a better idea of the size of the group would be gained by a census of the plants which are parasitized.

HABITAT AND DISTRIBUTION

The rusts are obligate, *i.e.*, strict parasites upon flowering plants and ferns, and are likely to be found anywhere that these hosts occur. Although the individual spores are microscopic they are usually produced in such quantities that when they break forth from beneath the surface of the plant they become evident or even conspicuous. The

sori with their spores may appear upon any part of the host-plant above ground. In rare instances spores may remain concealed within the tissues of the host. The presence of rust is indicated in many instances by yellow or discolored spots on the leaf-blades, by swellings and galls on the petioles and stems, or by the production of groups of supernumerary branches known as witches' brooms.

It is quite natural, as has been done in the preceding paragraph, to fall into the habit of speaking of the spore-structures as if they constituted the whole plant instead of being only the reproductive portions. Since these fruiting portions are at one and the same time the easily available and the distinctively characteristic parts of these plants it is possible much of the time to ignore the less evident vegetative parts. Taxonomic considerations are at present based almost exclusively on the spore-structures. A more complete study, however, must consider the plants in their entirety, that is, the vegetative mycelium as well as its diversified fructification.

Rusts attack plants in all sorts of localities from sea-level to the summits of high mountains, from swamps to desert areas, and from the tropics to the polar regions. Wherever there exists a vegetation of the higher plants usually some rusts occur. These ubiquitous parasites are to be found in the fields on cereal, vegetable and forage crops; in the forests on spruces, firs and oaks; in low places and swamps on sedges and crowfoots; in semi-arid regions on sagebrush and greasewood; in wild and waste places everywhere on ferns, grasses, legumes, sunflowers, asters, golden-rods, dandelions, and hundreds of other weeds and flowers. There is scarcely a family of flowering plants in which some of the members are not affected by one or more of these fungi. The order Pandanales, of which the common cat-tail is our representative, and the Palmales, the palms, are notable examples of large alliances upon which no rusts are at present known.

Because a rust occurs upon a certain kind of plant it does not follow necessarily that the distribution of the rust will be co-extensive with the distribution of the host. In the United States and Canada there are several species of rusts known on the wild roses. One species of rust, *Earlea speciosa* (*Phragmidium speciosum*), is practically everywhere that its rose hosts occur, while the related species of Phragmidium on roses are restricted to certain geographic areas, one being in the northeastern states, another in the plains region of the central states, another in the Rocky mountain region and so on. It is evident that the same environmental factors which determine the distribution of the higher

plants may not have the same influence, at least they cannot operate in the same way, on the distribution of parasitic plants.

In the cases of heteroecious rusts, where two distinct sets of hosts are involved, the distribution of a rust might be expected to be limited to the region in which both hosts are common, but the fact that many of these forms have the capacity to maintain themselves independently on one host by means of repeating spores upsets this expectancy. A notable illustration of this is the case of the carnation rust, *Uromyces caryophyllinus*, one stage of which on a European spurge has never been found in America. Several of the rusts of conifers will perpetuate themselves most successfully by means of their urediniospores on some of their alternate hosts. For example, *Coleosporium solidaginis* may be common on such hosts as asters and golden-rods in areas far removed from the other, the coniferous hosts.

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CHAPTER II

HISTORICAL REVIEW

Dawn of knowledge regarding the rusts; allusions to rust by the early Roman and Grecian writers; observations by Grecian and Roman scholars; the middle ages; introduction of the microscope.

From Micheli to de Bary; early interpretations; spontaneous generation; discovery of mycelium; parasitic fungi as cause of disease; wheat rust and the barberry bush; rise and progress of taxonomy; Persoon; Link; Fries.

Advance made by de Bary (1853–1863); laboratory study; culture work; tracing life-histories; new terminology; heteroecism; alternation of generations.

The modern period; polymorphism and change of hosts; long- and short-cycles; predicting kind of spores in a cycle; symbols to denote spore-stages; introduction of cytology; sexuality.

Terminology of the rusts; as applied to the vegetative body, mycelium, promycelium; as applied to the reproductive structures, sorus, stroma, peridium, paraphyses, hymenium, spores.

Physiology and specialization; pathology of parasite and host; teratology; the economic problem.

DAWN OF KNOWLEDGE REGARDING THE RUSTS

In beginning a historical account of the rusts as recorded in literature a common assumption regarding their antiquity requires a few words of comment. Reference is frequently made to the supposed allusions to rusts found in the Bible. Probably the earliest mention of this sort is in the exhortation of Moses to the Israelites just before their entry into Canaan (Deut. 28 : 22), which would place the date about 1360 B.C. Again there is a similar allusion in the prayer ascribed to Solomon offered at the dedication of the temple, which event probably occurred near the middle of the tenth century (I Kings 8 : 37; II Chron. 6 : 28), or about 950 B.C. Still later the prophets Amos (4 : 9) and Haggai (2 : 17) use the same expression. However, modern scholars believe that these passages did not assume their present form, and were not published, or possibly not written, earlier than five or six centuries before Christ, and that the expressions should not be credited to an earlier date. In each case two words "blasting" (or "blight") and "mildew" are linked, with the implication of injury to crops.

The Hebrew word shiddāphôn, rendered both in the King James and the Jewish[1] Bible as "blasting," in the original Hebrew signifies

[1] Official Bible of the Reform Jewish Movement, issued by the Jewish Publication Society.

drying up or scorching, and undoubtedly refers to a common injury of crops in the eastern Mediterranean region, due to the hot sirocco from the Arabian desert. That this is the correct interpretation is clearly shown by another passage. The same Hebrew word, but as a verb, occurs in Genesis 41 : 23, 27, where it is recounted that Pharaoh saw in a dream seven ears [of wheat] "blasted with the east wind," or according to the American translation "blasted by the east wind." It is clear that there is no reference here to smut, rust, or any fungous disease.

The Hebrew word yērākôn, rendered as "mildew" in nearly all Teutonic translations of the Bible, in the original Hebrew signifies yellowness or pallor. The corresponding word in Syrian and Arabic is best rendered by jaundice. In each case the underlying idea is that of a sickly or enfeebled appearance. The Hebrew word is used only in one other place in the Bible, Jeremiah 30 : 6, where it describes the wan appearance of the faces of men who are in great fear or pain, and is translated both in the King James and the Jewish versions by the word "paleness:" "all faces are turned into paleness," or in Moffatt's translation of 1925, "to a deadly pallor."

It is highly probable that at such early times descriptive terms would have been applied to the general symptoms of disease or injury, and not to the small differences shown in connection with certain abnormalities. The words "blasting" and "mildew" quite likely are to be accepted as meaning general injuries to crops, brought about by hot dry winds in the first instance, and in the second instance by extremes of weather, insects, parasitic fungi (possibly including rust), and various other diseases and hindrances to normal growth. Both the context, and the meaning of the Hebrew words as independently used elsewhere in the Bible, bear out this interpretation Such an interpretation is also supported by many able lexicographers.[1]

The specific meaning of smut and rust, sometimes inferred, as in some English, German and other editions of the Bible, and sometimes expressed ("sot och rost," as given in early Swedish translations), must be ascribed to the natural tendency to read into ancient authors ideas that only a much greater advance in knowledge could have made possible. We believe it best, therefore, to dismiss Biblical references as having little or nothing directly to do either with the Ustilaginales

[1] *Cf.* Gesenius, Hebräisches und Aramäisches Handwörterbuch über das alta Testament. 6er Aufl. 1915; Murray, New English Dictionary, vol. 3, pt. 2, p. 435. 1908; Hastings, Dictionary of the Bible, **3** : 368. 1903; and others.

or the Uredinales, and as better explained by natural causes wholly or largely other than smuts or rusts, although this is not the opinion held by Eriksson (Eriksson & Henning, 1896, p. 7) and many other writers.

Allusions to rust by the early Roman writers. — A legendary account of the rusts, quite disconnected from the mythical one of the Bible, and carrying the hypothetical record far back into the misty, unrecorded past, is brought to our attention largely through the writings of Roman scholars, who flourished in or near the brilliant Augustan age (43 B.C. to 17 A.D.).

In the early days, especially of the Roman Republic (510 to 29 B.C.), when the inhabitants of the cities were largely dependent for food upon the products of near-by fields, the not infrequent scourge of rust naturally arrested the attention both of urban and rural dwellers. Among the Romans there were many religious festivals,[1] instituted for the purpose of imploring the powers above, their gods, to assist in promoting human interests. Several of these occurred in April, especially those pertaining to husbandry. Of these the Fordicidia on the fifteenth had to do chiefly with herds, the Cerealia on the nineteenth with crops, the Parillia on the twenty-first with flocks, and the Robigalia on the twenty-fifth, when the wheat began to head, with the rust.

The Robigalia, together with other religious festivals, is reputed (*fide* Pliny and Tertullian) to have been founded by Numa Pompilius, second king of the Romans, at a time as early probably as 700 B.C. Indicative of great antiquity, and as customary in early times, the name of the rust god was not specifically designated as male or female, but both forms of address were used, hoping thereby to avoid giving offense. Ovid uses the form Robigo, but others among the older writers use Robigus.

The best account we possess is by the poet Ovid in his "Factorum Liber IV," who personally witnessed a ceremonial at about the time of the opening of the Christian era. This took place in the grove dedicated to the god at the fifth milestone out from Rome on the Via Claudia. The lengthy prayer of the officiating priest is given by Ovid in exquisite Latin verse, and begins:

> "Stern Robigo, spare the herbage of the cereals,
> . . . . . .
> . . . withhold, we pray, thy roughening hand."

[1] *Cf.* Fowler, W. W. The Roman festivals of the period of the Republic. London, 1899.

The word here given as "roughening," is sometimes translated "rusting." There is no exact English equivalent. It implied the production of scabs, sores, or abrasions of the surface, and could scarcely have meant anything other than stem rust.

The Robigalia deteriorated under the Empire from a ceremony of real import as conducted during the days of the Republic, but survived in modified forms for centuries, with traces still to be found in the litany of the Christian church. Underlying the ceremony was primarily not the idea of a revengeful deity, as often stated, but the belief that the power that could create the rust would also be able to control it. It was in essence the same feeling that actuates the religious ceremonies of the present day when prayers are offered to the supreme power above to avert injury to the crops from drought, floods, or other natural causes.

Allusions to rust by the early Grecian writers. — The attention given to rust among ancient people of the eastern Mediterranean region was by no means confined to the Romans. It is incidentally mentioned that in the worship of Apollo at Rhodes (Strabo 613) the god was given the cult-title ἐρυθίβιος, or "Apollo of the Rust," and again in the worship of the goddess Demeter in Asia Minor a similar cognomen was used (Styrzius 210). The Greek word ἐρυσίβη, *erysibe*, from which these titles were derived, is the equivalent of the Roman word *robigo*, which besides the usage here cited had a primary meaning of rust of metals and carried the idea of redness. It was misapplied as a generic name by Linnaeus, DeCandolle, Link, and many later authors to the powdery mildews, from which the genus Erysiphe and family Erysiphaceae arose. Wallroth (1833, p. 193) attempted to establish the generic name in the Grecian sense, as used by Theophrastus, but was not supported.

Observations by Grecian scholars. — The earliest Greek records ascribable to direct observation are those of the two great contemporaneous philosophers of the palmy days of Alexander the Great, Aristotle (384–322 B.C.) and his associate, Theophrastus (373–286 B.C.), the latter being the most accurate observer of cultivated and wild plants among the ancients.[1] Aristotle ("Probl. sect." and "De animal. hist.") speaks of rust (ἐρυσιβη) being produced by warm vapor, of devastating rust, and of rust years. These references may possibly include any rusty appearance, but Theophrastus ("De causis planta-

[1] Greene, E. L. Landmarks of botanical history. Smithsonian Misc. Coll. **54**[1]: 329, 1909.

rum") is more specific, for he says that cereals are more affected by rust than are legumes, and barley more than wheat, the variety of barley called "Achilles" being most susceptible.

Observations by Roman scholars. — No similar records are available for the next three hundred years, until we come to the Roman authors of the Augustan period, who wrote during the century which included the beginning of the Christian era.

Virgil said (about 25 B.C.): "*Mox et frumentis labor additus; ut mala culmos esset robigo*" (Georgics I, line 151), which clearly means that rust injures the grain by attacking the culms, *i.e.*, stems and sheaths. However, the word *robigo*, like the English word rust at the present time, was loosely applied, and might have included other kinds of fungi. Varro (writing about 35 B.C.), probably the most reliable and accurate observer among the writers on agricultural topics of the Roman Republic, implores Robigus and Flora to protect the grains and trees from rust ("*neque rubigo frumenta, atque arbores*"). Columella, writing about a century later, in his "Scriptores rei rusticae" speaks of means for averting rust (I, Chap. 5), yet in his "Liber de arboribus," he has a chapter headed "Ne robigo vineam vexet," which certainly did not refer to the Uredinales. Pliny (23–79 A.D.) in his "Natural History"[1] calls rust the greatest pest of the crops ("*robigo maxima segetum pestis*").

Absence of data during the middle ages. — Following the Roman writers of the first century a long interval of about fifteen hundred years elapsed with no important record pertaining to the rusts. Doubtless the crops were ravaged by rust as much during this period as before and after, but the times did not lend encouragement to such observations and records. This long period embraced the dark ages of history and the silent ages of science.

No change in views during the 17th century. — There are plenty of indications that certain species of rusts were of recognized economic importance during the seventeenth century, and a source of general interest, although exact records cannot be cited. But no material advance was made in their consideration over the conceptions or methods of the ancients until the introduction of the microscope. When it became possible to see more than the unaided eye or the simple lens could reveal, an added interest and refinement of discrimination gave decided impetus to this line of observation.

[1] *Cf.* Greene, Landmarks of botanical history, 1909, pp. 155–159.

INTRODUCTION OF THE MICROSCOPE

The suitable combination of two unlike lenses to increase the apparent size of small objects originated in Holland about the year 1590, but the instrument was not called a microscope until 1625, the name

FIG. 33. — Earliest illustration of a rust as seen under a microscope: teliospores of *Phragmidium disciflorum* on leaf of garden rose. (After Hooke, 1665.)

being given by Giovanni Faber, an Italian of the Accademia dei Lincei. It did not come into sufficiently general use materially to influence observations upon microfungi for a century after its invention.

Only two illustrations of rust were published previous to the early part of the eighteenth century. Robert Hooke of England issued from a London press in 1665 the results of his microscopic observations in a large folio volume entitled "Micrographia," which was many times reissued. Among the marvelous things thus revealed was that of teliospores of *Phragmidium disciflorum* from the leaf of a common garden rose, under a magnification of about 150 diameters (Fig. 33). Not long afterward (1675) Malpighi of Italy issued a less sumptuous work, also from a

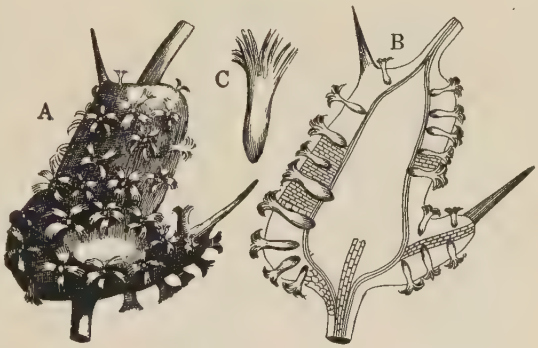


FIG. 34. — "Flowers" on twig of English hawthorn: *A* surface view of the tumor bearing numerous "flowers," the aecia of *Gymnosporangium clavariaeforme* with their peridia reverted; *B* section of same; *C*, one of the "flowers" more enlarged. (After Malpighi, 1675.)

London press, under the title "Anatome plantarum," which included in one of the chapters, headed Tumors and Excrescences, an illustrated account of a tumor bearing "flowers" (Fig. 34) on twigs of English hawthorn, the so-called "flowers" being in fact the aecia of *Gymnosporangium clavariaeforme* on *Crataegus oxyacantha.* The author says he had seen such swellings also on the leaves of the same host, and similar ones on Urtica (aecia of *Puccinia caricis*), and other plants.

FROM MICHELI TO DE BARY (1729-1853)

It was not until 1729 that the microscope became an indispensable aid in the discrimination of small fungi. In that year appeared the "Nova plantarum genera" of Micheli, Director of the Botanic Garden in Florence (Fig. 35). The work was an example of good scientific method for the time. The genera of flowering plants, ferns, mosses, lichens, algae and fungi, both large and small, received equally serious consideration. Spores of the larger fungi were germinated, grown, and the mycelium and sporophores observed.

The first genus of rusts. — The genus Puccinia, named in honor of a Florentine physician and teacher, established by Micheli with description and illustration (Fig. 36), became the first genus of the Uredinales. It was founded upon the telia of *Gymnosporangium clavariaeforme* on Juniperus. The name Puccinia was afterward bandied about by various writers without regard to earlier usage, as was the habit among botanists of the time and for many years thereafter, and finally became settled upon the rusts that bear more or less resemblance to *Puccinia graminis.* From the time of Micheli illustrations to accompany descriptions of rusts became increasingly frequent (Fontana 1767; Tode, 1790; Persoon, 1794).

Early interpretation of microscopic appearance. — In trying to interpret the appearance of the microfungi as seen under the microscope the parts of the fungus were naturally likened to parts of flowering plants. The sporeheads or large spores seemed like the fruiting pods of Lilliputian plants, each containing its quota of seeds. This was comparatively easy to demonstrate in case of molds (Mucor), and from analogy it seemed not improbable in case of the rusts. Thus Robert Hooke (1665) explained the teliospores of the rose Phragmidium as pods (*cods* in old English) of a minute vegetable, in all probability containing seeds, and "if these cods have a seed in them so proportioned to the cod as those of pinks and carnations and colum-

bines, and the like, how unimaginably small must each of those seeds necessarily be." DeCandolle in 1807, speaking of the spores of Uromyces and Uredo says that "with a microscope this powder seems composed of ovoid or globular pericarps . . . filled with many small grains that are considered spores," and also that each cell of a teliospore "contains at least 100 such 'spores'." This reproductive powder, "or animated dust" as it is styled by Sir Joseph Banks (1805), is figured in the famous letter on wheat rust sent out by him to the farmers of England (Fig. 37). This interpretation was, in fact, generally accepted by most mycologists and other writers for nearly a century, including Fries, Léveillé, and even by such careful observers as the Tulasne brothers (1847). The strong presentation by de Bary (1853) brought about its ultimate suppression.

Fig. 35. — Statue of P. A. Micheli in the portico of the Uffizi palace, Florence, Italy. The right hand holds his volume of "Nova plantarum genera," and the left hand a sprig of laurel, while laurel, an agaric and a boletus lie on the pedestal.

Germination of rust spores. — Although the germination of spores of higher fungi had been observed by Micheli and others, yet the first instances among microfungi were recorded by Prévost (1807), using *Uredo alliorum, U. linearis,* and spores of Tilletia and Cystopus, and the first illustrations were made by Corda (1839), using aeciospores of *Aecidium tussilaginis.* Pores were not observed until 1847 when the Tulasnes noticed them in both urediniospores and teliospores and called them "pores or oscules" (Fig. 38). The germination of teliospores with their promycelia was first figured

(Fig. 39) and correctly interpreted by the Tulasnes (1847), although Unger (1833) had earlier seen and figured such germination in Cronartium (p. 62), but had given an erroneous interpretation.

Belief in spontaneous generation. — The most diverse views have been held of the nature and origin of the microfungi. That they arose by some form of spontaneous generation was a very ancient

Fig. 36. — *Puccinia non ramosa*, as illustrated in Micheli's "Nova plantarum genera": telia scattered over trunk and branches of *Juniperus sabina;* healthy branch and cone above to the left; whole and truncated sori below; teliospores at lower right. (After Micheli, 1729.)

belief, which was later adopted by botanists and one which the majority of them did not relinquish until the middle of the nineteenth century. Even after that there were still a few adherents to the theory, and among the unlettered the belief is often met with at the present time. In its crudest form it is found in Bock's Herbal of 1560, as quoted by Sachs (1890): "Mushrooms are neither herbs nor roots, neither flowers nor seeds, but merely the superfluous moisture of the

earth and trees, of rotten wood and other rotten things. From such moisture grow all tubera and fungi."

A connection was early observed, even as today, between the weather conditions and the abundance of fungi and especially of grain rusts. Pliny says in his "Natural History" that rust is due to hot sun on the grain when wet with dew. The influence of the sun was variously

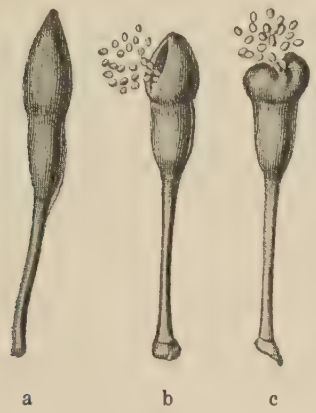


Fig. 37. — Early conception of spores of *Puccinia graminis*, each considered to be an independent plant: *a* mature "plant," *b* bursting to discharge the "spores" or "animated dust," *c* "spores" discharged and "plant" collapsed. (After Banks, 1806a.)

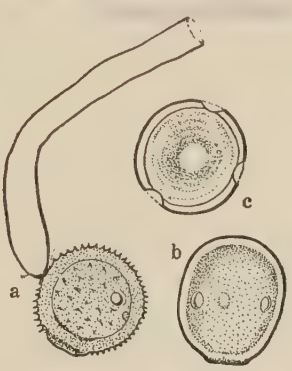


Fig. 38. — Pores or "oscules" in urediniospores of *Puccinia suaveolens*, as drawn by Tulasne: each spore with three equatorial pores, *a* with germ-tube, *b* side view, *c* end view with hilum indicated in center. (After the Tulasnes, 1847.)

interpreted, but most often considered to have some action on the sap in the plant. Robert Plot of the Ashmolean Museum (1686) found an explanation for the rust in the excessive richness of soil that "sending up a moist viscous steam that upon congelation in the air falls down upon the corn, and there sticking to the straw and further hardened by the sun, so binds up the pores that the nourishing juice is prevented thereby ascending to the ear." Some thought, like Hooke (1665), that for some cause sores form under the epidermis where the tissues "putrify, as it were, so that the moisture breaks out in little scabs," and gives a soil for the fungus. The astute English farmer, Jethro Tull,[1] suggested that insects brought by the east wind doubtless incited the abnormal change by their punctures. Insects, atmospheric

[1] Tull, J. Horse-hoeing industry. Ed. by William Cobbett. 466 pp. 1729.

electricity, rains, rapid changes of temperature, wounds, and numerous other inciting causes had their advocates.

Exanthematic transformation. — The belief that the endophytic fungus could be directly developed in an exanthematic manner did not prevent a taxonomic treatment of the microfungi. According to this theory the fungus originated from the excessive accumulation and condensation of sap, as pus is derived from an inflamed spot in animals, as believed by Unger (1833), or the tissues of the host were indirectly transformed into the fungus, as held by Fries (1832, p. 505), Meyen (1841), and others. Persoon (1818), one of the most discriminating of the early mycologists, while believing in spontaneous generation, also believed that when once formed each kind was capable of perpetuation by means of its spores. Only a few scholars, like Losana (1811) and Turpin (1835) denied the fungal nature of the rusts, but the most diverse and extraordinary views were held regarding their true character up to the middle of the last century, and that despite the able exposition by Ehrenberg in his "Epistola de Mycetogenesi" in 1820. Whatever particular explanation might be entertained to account for the occurrence of endophytic fungi there was quite a general belief in a predisposition of the host. Either the host acted to engender the fungus or it exerted a selective influence. In this way the presence of a rust on some plants and not on others even when nearby, was accounted for.

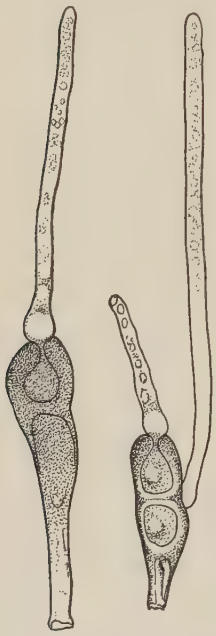


Fig. 39. — Germinating teliospores of *Puccinia cirsii-oleracei*, producing promycelia. (After the Tulasnes, 1847.)

Discovery of mycelium. — The cobwebby or felted growth of many fungi was early observed by botanists, and called "byssus." As a genus (Micheli, 1729; Linnaeus, 1737; Gleditsch, 1753; *et al*, in part changed to Hypha by Persoon, 1822) Byssus was made to include many diverse things, *e.g.*, Gymnosporangium on Juniperus (Linnaeus, 1737), and was by no means confined to the fungi. Although the name of mycelium was first used by Trattinick in 1809 in his work on "Edible Fungi," such a growth was not recognized in connection with the rusts until thirty years later (1839), when it was detected by Léveillé and Corda at about the same time, but independently. Such a growth had

long been suspected, for Banks (1806a p. 53) says the spores of the grain rust gain admission to the host through the breathing pores, where "they germinate and push their minute roots, no doubt (though these have not yet been traced), into the cellular tissue."

Means of propagation. — Those who believed the rusts due to a diseased condition of the host, as well as some others, took the view that they possessed no direct means of propagation. Others held that the minute "seeds," "spores," "animated dust," which were assumed to be within the spores proper, when spread by the wind, found entrance into the host and developed into the fungus. Two opposing views were held in this connection regarding the way the ultra small "spores" gained entrance into the host. One view, made prominent by Banks (1805), considered that the impalpable "dust" or "corpuscles" from the spores fell upon the leaves and entered through the breathing pores. The other view, as stated by DeCandolle (1807), found it "more plausible to think that the 'spores' of fungi fall to earth at their maturity, are mixed with the dirt, drawn in by the aspirate sap, enter the roots, pass up the woody portions of the plant by the pith tubes, and arrive with the sap in the herbaceous parts, where finding a position of convenient nourishment, the 'spores' develop." This latter theory was supported by Prévost, who had nevertheless seen the true germination of the spores, and by Fée and especially Léveillé. It was believed by those who had seen the spores germinate that the hypha produced by the germination of a spore divided itself into numerous "molecules," which acted the same as the fine "particles" that others believed were discharged directly from the spore. It was not until the direct entry of the germ-tubes through the stomata had been seen by Corda (1839), Bonordon (1851), and repeatedly by the Tulasnes (1847), that this theory was overthrown.

Parasitic fungi as cause of disease. — The early opinions and observations pertaining to rusts as disease-producing organisms of economic importance centered largely upon the stem rust of cereals. The early works on plant pathology (Zallinger, 1773; Plenck, 1794; Werneck, 1807) make no mention of parasitic fungi, or of any disease that might be ascribed to them. They were not generally considered true causes of disease until the middle of the nineteenth century. Nevertheless, the unlettered and the non-botanists found reason to look upon the rusts as a menace to crop production. If wheat rust (mildew) had not been familiar at the beginning of the seventeenth century, it would have been a meaningless speech that Shakespeare prepared for his

actor in 1602 (Lear III. iv. 123), in which rust is made one of the score or more of misfortunes that the "foul fiend" is accused of wreaking on man, beast and inanimate things.

The barberry bush, a native of the mountains in central and western Asia, was taken to Italy and Spain by the Arabians in the seventh century, but it was not until the seventeenth century that it was introduced[1] into northern Europe and North America, and became popular for its fruit and as a hedge plant (Lind, 1915). Soon thereafter injury to cereals growing near the barberry plants began to receive attention.

A wide-spread belief of husbandmen in northern Europe and eastern North America at the beginning of the eighteenth century and possibly earlier, that the barberry bush increased the rust on wheat in its vicinity, may be inferred from the early restrictive laws against barberry passed in both Europe and America (p. 43). The earliest carefully recorded observations bearing on the probability of such an association appear to have been made by Marshall in the years 1781 (1787, p. 21), 1782 (1787, p. 395), and again in 1784 (1790, p. 11) in northern England, which confirmed the prevalent opinion of the region that the barberry is injurious to wheat, but he says that he "was not able to form any probable conjecture as to the cause of the injury" (1790, p. 13). The presence of aecia on the barberry plants is not mentioned, and probably was not observed.

Persons in various parts of Europe and America up to the middle of the nineteenth century and later contended that the barberry was unjustly accused, and among those who considered it guilty some ascribed the baneful influence to the bush itself and others who had observed the minute cup-fungus found upon its leaves directed attention to the parasite it harbored. The theory of a connection between the barberry bush and wheat rust became more and more confirmed in the minds of cultivators, although uniformly opposed by mycologists.

The first record of a well-directed effort to show connection between the fungus on the barberry and rust on cereals appears to have been made by Knight (1806), an eminent English horticulturist (*Cf.* Ramsbottom, 1913). He sowed wheat in the fall of 1804 around a barberry bush in his garden, some of the same wheat being sowed at a consid-

[1] The apparently natural conditions under which feral plants of barberry often occur both in Europe and America have frequently led to the belief, especially in northern Europe, that the species is native. *Cf.* Dunn, S. T., Alien flora of Britain. 1905.

erable distance from any barberry. All the wheat plants remained healthy until July, 1805, when those next the barberry showed signs of disease. Examining the barberry, he found "upon its fruit a species of fungus similar in color to that on the straws of the wheat." "I was," he says, "much disposed to believe them parasitical plants of the same species," their differences, he thought, being due to the influence of the hosts. Since the wheat that grew at a distance from the barberry remained perfectly healthy, he carried a branch of the barberry "with diseased fruit upon it," and sprinkling it with water brushed it over the healthy wheat plants, repeating this on three successive days. In ten days rust appeared on the treated wheat plants and on no others.

The second attempt to demonstrate a connection between the cereal and barberry rusts was made by Schøler (1818), a Danish schoolmaster, who from 1813 to 1817 planted barberry bushes in grain fields and invited the public to come and view the results. In 1816 he tried the experiment of carrying a branch of heavily rusted barberry, well wrapped up, into a rye field wet with dew. He touched the moist leaves of rye with the affected barberry, marking the plants. In five days the marked leaves showed the rust, which appeared nowhere else in the field.

This completes the few recorded experimental attempts to connect barberry and wheat rust up to the time of de Bary. As no one could give a satisfactory explanation of the transformation of the barberry fungus into the very unlike wheat fungus, and as all mycologists and many others opposed the idea as preposterous, it is no wonder that the agriculturists had a hard fight in their attempts to banish the barberry. It is reported that a law against it was enacted in the north of France at Rouen in 1660. In America laws were enacted in Connecticut, Rhode Island and Massachusetts between 1726 and 1766. After some years the Connecticut and Rhode Island laws were renewed for a time. Several European countries passed similar laws shortly after 1800. In Denmark the feeling of the farmers against the growing of barberries reached such a height that in 1805 a bitter feud broke out between those who believed the bush was injuring their crops and those who defended it, which continued for sixty years. The early history of the belief in the theory and of the struggle of the farmers against the barberry is given at some length by Nielsen (1877), Eriksson and Henning (1896, pp. 12–21), Klebahn (1904a, pp. 205–221), and especially by Lind (1915).

Rise and progress of taxonomy. — The early taxonomic disposition of the rusts, by which they were classified like other objects of natural history, was not materially influenced by the opinions which their authors held regarding their origin, nature and development. Each form was described according to its appearance, more and more in detail as improved lenses became available. Those that sufficiently resembled one another were placed in the same genera, and these genera were variously distributed.

Only a few kinds of rusts and smuts were recognized by Linnaeus and they were variously distributed with other small fungi, algae, or even in the animal kingdom with infusoria (*Dissertationis mundis invisibilis*, 1769). He was not interested in fungi, was even their sworn enemy, according to Wallroth. Nevertheless, he had a considerable following, especially in Sweden. Wahlenberg in his several floras of Sweden from 1812 to 1826, and later, made no changes. The first attempt at an orderly arrangement of fungi was by Persoon in 1794.

Persoon's contribution to taxonomy. — Persoon (1794) placed all fungi in two classes: Angiothecium and Gymnothecium. Three genera of rusts were recognized: Aecidium, which was established by Persoon three years previously, together with Uredo and Puccinia, which were now described as new. These are the only rust genera for the 65 years since Micheli's solitary genus. The genus Puccinia, as interpreted by Persoon, was placed in the second class (Gymnothecium) among the fleshy fungi. It included telial forms of species that are now distributed under Phragmidium, Gymnosporangium, Puccinia, both macro- and microcyclic species, and also Uromyces. The other two genera, Aecidium and Uredo, were placed in juxtaposition in the first class (Angiothecium). Altogether 77 genera of fungi were recognized. In 1797 this article by Persoon was reissued in independent form, and without change except in the wording of the title, but with 28 pages of comments added. In these comments Persoon suggested that the genus Puccinia by its structure and habit more properly belonged in the first class with Aecidium and Uredo. This early classification of the fungi is essentially unchanged in the author's more detailed work of 1801.

The credit of first recognizing the rusts as a distinct group must be accredited to Persoon, for he not only was the first after the beginning of binomial nomenclature to establish genera among the rusts, where for a time he admitted no other forms of fungi, but in 1818 (*l.c.*, p. 50)

he said, writing in French, "a small but very natural family, very rich in species is that of the *Urédinées*, all parasitic, mostly under the epidermis of green leaves." The authors of important works who followed Persoon's classification in the main were Schumacher (1803), Rebentisch (1804), who established the genus Roestelia, Albertini & Schweinitz (1805), DeCandolle (de Lamarck & DeCandolle, 1805), who established the genera Gymnosporangium and Bullaria, Schweinitz (1822) and Brongniart (1824). The last author is generally given the credit of proposing Urédinées for the name of the group.

Link's contribution to taxonomy. — In 1809 Link brought out a new classification, and at the same time established the genus Podisoma and the omnibus genus Caeoma with its subgenera Aecidium, Roestelia, Uredo, Ustilago and the new subgenus Caeomurus. The larger groups of various grades received new names. A second paper in 1815 under the same title gives his later views. In this he changes the name of his omnibus genus from Caeoma to Hypodermium, adds to it the subgenus Peridermium, and substitutes Uromyces for Caeomurus. He also establishes the genus Phragmidium and suppresses Podisoma. He had previously placed all the rusts under the Endophytae, fungi that grow in living plants, but he now takes a backward step and removes Gymnosporangium from that division to become associated with Tremella. His still later, and one might possibly say more mature, arrangement is that of 1825, in which he establishes Triphragmium and restores Podisoma. He unblushingly throws over Hypodermium as a genus of rusts and makes it a genus occurring on dead leaves and twigs of pines and firs, "*a Caeomate differunt.*" He also restores Caeoma, as a genus, but abandons all of the subgenera, so that, *e.g.*, *Caeoma Aecidium Euphorbiae* becomes plain *Caeoma Euphorbiae*, etc. Such a futile ending has been the fate of all subsequent attempts by various authors to establish a duogeneric method for showing relationships among the rusts.

Many authors accepted Link's classification, either wholly or in part, but often with minor modifications. Nees von Esenbeck in 1816 added Dicaeoma as a subgenus to Link's Caeoma. In the following year appeared Martius' "Flora Erlangensis" in which he added Roestelia to Link's Caeoma, and also changed the group-name Mucedines to Coniomycetes, a term that was used by most authors for many years afterward. Possibly Schweinitz (1832) in his "North American Fungi" may have been the last to use the cumbersome names introduced by Link. Link's classification was accepted by Schlechtendal

(1824), and in part by many others, including S. F. Gray (1821) in England, and Wallroth (1833) in Germany.

Fries and his followers. — In 1832 Fries' "Systema Mycologicum" had reached its third volume, closing with the Coniomycetes. Fries was a disciple of Linnaeus, and not only had a poor opinion of the parasitic fungi but an antiquated conception of their nature. He characterizes the Hypodermii (*l.c.*, p. 504) in this wise: "No proper vegetative body; sporidia originating from the metamorphose of the cellular structure of living plants: an inferior kind of fungi." The name Hypodermii to replace Endophytae is used for an order which is made to include most of the rusts, smuts and some other fungi, but not his new genus Aregma (of which Phragmidium is made a subgenus), and the genus Xenodochus of Schlechtendal. His two new genera Aregma (*l.c.*, p. 495) and Epitea (*l.c.*, p. 510) were not well founded, and are now placed in synonymy. Such was the prestige of Fries that notwithstanding his imperfect knowledge of the group there were many who accepted his leadership, among whom may be mentioned Endlicher (1836), Léveillé (1839, 1847), Corda (1842), Rabenhorst (1844), Strauss (1850), Berkeley (1857, 1860), and Cooke (1871). Each of these authors made changes in the arrangement of the genera. Léveillé (1847) separated the Uredineae into those (1) with paraphyses, which he called "cystidia," (2) without paraphyses, and (3) doubtful Uredineae. The last included Melampsora of Castagne and genera not now included in the rusts. In the second group beside the rusts many smuts were included together with Cystopus. In the first group are only three genera, newly erected: Lecythea, Physonema, and Podosporium. They are distinguished by the disposition of the paraphyses in the sorus and whether the spores are pedicelled, sessile, or in chains. The new genera met with considerable favor, especially from those who were more interested in finding readily recognizable diagnostic characters than in the employment of more subtle characters indicating relationship.

ADVANCE MADE BY DE BARY (1853-1863)

We have now arrived at a decade that ushers in a conspicuous epoch in the development of knowledge pertaining to the rusts. The empiricism and shifting theories that heretofore largely prevailed are for the most part abandoned. The careful study of the orderly development of a few species is substituted for the prevailing method of comparing the gross appearance of many forms. The recognition of a mycelium

homologous with the vegetative body of larger fungi, and in like manner bearing fructifying structures, set forever at rest the age-long controversy about origin through transmorphism or by spontaneous generation. And especially the cultural demonstrations showing that the rusts produce in definite order a succession of unlike spore-structures, previously regarded as belonging to separate genera, marked the change from the old to the modern point of view.

Biographic data. — Not the least interesting item in this intellectual revolution is that it was inaugurated by a young man scarcely twenty-two years old, not yet at the end of his university course. Heinrich Anton de Bary (Fig. 40) was born January 26, 1831, in Frankfurt-on-the-Main, of Belgian parentage, his father being a physician. During his school days he was a diligent collector of plants and also increased his herbarium by exchanges. He thus laid a substantial foundation for his subsequent botanical career by an intimate knowledge of the native flora. He also became interested in the fungi during this time through Fresenius, a physician and teacher in Frankfurt, and a mycologist of note. After studying in the universities of Heidelberg, Marburg, and Berlin, he received on March 30, 1853, the degree of doctor of medicine, his thesis being on the sexual reproduction of plants. He now returned to Frankfurt as a practising physician, but in December of the same year accepted a lectureship in the University of Tübingen, where he was associated with Hugo von Mohl, the foremost histologist of the time, author of the term protoplasm, a skilled microscopist and accurate delineator of microscopic objects. From there he soon went to Freiburg, Halle, and finally to Strassburg.

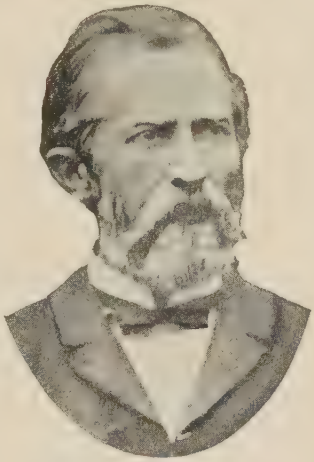


Fig. 40. — Portrait of Anton de Bary.

Before graduation de Bary published one paper on fungi, a study of *Achlya prolifera*. About the time of graduation he issued his famous work "Die Brandpilze" (April 1, 1853), dealing with rusts and smuts, which was prepared during undergraduate days. It is this work and the one which followed ten years later that gave the chief impetus to the modern phase of uredinology, and placed the author among the

foremost leaders in the development of a knowledge of the rusts. The particular reasons stated for undertaking these studies were the interest of agriculturists and botanists in the smuts and rusts as affecting crops, and the many controversies regarding their relation to plant diseases, whether they were the cause or product of the same. Yet de Bary was not primarily a plant pathologist; his interest lay much more largely in morphology.

Laboratory study. — In the first paper (1853) de Bary presents a careful study of Ustilago (four species), Protomyces, Cystopus, and rusts of a dozen or more species, which forms the basis of his pronouncements. Beside using an excellent microscope, he employed microchemical reagents, such as sulphuric and nitric acids, chlor-zinc-iodide, potassic hydrate, iodine, sugar, and other solutions, obtaining the suggestion from Tulasne who had used sulphuric acid. By means of these he demonstrated that the spot in teliospores, the so-called nucleus of Tulasne, sporidiolum of Unger, often shown in early illustrations, is in reality a vacuole. Spores are demonstrated to possess a wall, overlaid with cuticle, and enclosing endoplasm with oil drops and other substances. More important yet, the course of the mycelium in the plant is traced as abundant branching hyphae passing in various directions between the cells of the host. These hyphae gather at certain places and form the sori. Investigation of the comparative morphology of the several species is accompanied by a critical study of the works and opinions of previous authors. He comes to the conclusion that as the rusts have a mycelium arising from spores, and probably entering the host by the easiest way through the stomata, and as they reproduce themselves by means of their spores, they must be independent organisms, and therefore true fungi (1853, p. 124). From this standpoint they cannot be considered the result of disease in plants, but must be its cause. He gives much attention to the spermogonia, and is inclined to agree with Meyen that they are sexual organs. He thinks a decidedly different relationship exists between forms accompanied by spermogonia and those without, and places the former together under Aecidiacei. He does not accept the view of Corda, Léveillé, and others, that teliospores of Puccinia and Phragmidium are parasitic upon their uredinia (*l.c.*, p. 130). When one form of spore follows another in the same sorus, he says it is probable that there is a mixture of different kinds of mycelium, of which one and later the other fructifies. He was particularly hostile at this time to the wide spread belief that the barberry and cereal rusts have a genetic relationship.

Influence of the fundamental work of Tulasne. — Following closely upon the appearance of de Bary's notable contribution Tulasne (1854b) published a classification of the rusts, which has been the basis of all later arrangements up to the present time. He excluded the smuts, but included Cystopus with some misgivings. The true rusts are assorted under five groups, as follows: Aecidinei: Caeoma, Aecidium, Roestelia, Peridermium; Melampsorei: Melampsora, Coleosporium; Phragmidiacei: Phragmidium, Triphragmium, Puccinia, Uromyces, Pileolaria; Pucciniei: Podisoma, Gymnosporangium; Cronartiei: Cronartium. No one else had studied the morphology and development of the rusts with such thoroughness and discriminating insight regarding their true nature. His work had great influence with de Bary, as it has had with all subsequent students of the group.

Tracing the life-histories. — In opening his second paper on the rusts, after ten years of general teaching and research, de Bary (1863a) modestly states that knowing that the rust spores germinate as do those of other fungi, it remains to ask what becomes of their germ-tubes when they have found conditions favorable for further growth. In answer to this query he brings facts gathered from direct and carefully planned experiments and cultures, as well as from wide observation.

His successful cultures embraced *Uromyces fabae*, *U. appendiculatus* and *Puccinia tragopogonis*, using basidiospores and securing pycnia and aecia, and also using both aeciospores and urediniospores and securing uredinia and telia; *Puccinia coronata*, *Coleosporium campanulatum*, and *C. asclepiadeum*, using urediniospores and getting uredinia; *Puccinia dianthi* and *Endophyllum sempervivi*, using basidiospores and getting microtelia in the first species but systemic infection without maturity in the second. From these results he generalizes that each species of the rusts, from which group he excludes all other microfungi, "has two to five kinds of reproductive organs, which have coördination or a regular succession" (1863a, p. 69). He found that the germinating basidiospores grow into the host by directly penetrating the cuticle, except in *Puccinia dianthi*, where the entrance is by way of the stomata, and that the germ-tubes of aeciospores and urediniospores uniformly enter through the stomata. He reaffirms his earlier statements that the rusts are true fungi and do not arise by spontaneous generation, and that the hyphae pass along the walls and intercellular spaces, rarely penetrating the cells. He still thinks the spermogonia may be male organs, but can produce no proof.

Introduction of a new terminology. — As a direct result of his study de Bary (1865) introduced a new terminology for the spores of the rusts, which has prevailed in large part up to the present time. He had been using the terms proposed by Tulasne, with a few modifications, but found them inadequate for accurately designating the new relationships. Tulasne had considered the teliospores of most species to be "true spores," and had distinguished both aeciospores and urediniospores as "stylospores." De Bary now proposed the terms aecidiospore, uredospore and teleutospore (p. 67).

Alternation of hosts announced. — The cultures attempted by de Bary (1863a) that resulted unsuccessfully proved as interesting and significant as the others. These were *Puccinia rubigo-vera* (*Aecidium asperifolia*) and *Melampsorella symphyti* (*Uredo symphyti*), using aeciospores from *Lycopsis arvensis* and *Symphytum officinale; Puccinia graminis, Coleosporium campanulae* and *C. senecionis,* using basidiospores from *Triticum vulgare, Campanula rapunculoides* and *Senecio vulgaris.* In these cases, as in the successful cultures, the spores were sown on the same species of hosts from which they were taken. As these tests were conducted with the same precautions as the others, but resulted in no infection, he arrived at the conclusion that such instances "could be explained by the alternation of generation which requires the alternation of host plants." Having now gone so far he admits that "one comes around, perhaps, in a way, to the ancient opinion according to which rusted wheat would be infected by the rust of the barberry" (*l.c.*, p. 91).

The term "heteroecism" supplied. — Only a cultural demonstration was now required to confirm the logical conclusion reached by de Bary regarding the alternation of hosts. The next season, 1864, the cultural proof was obtained by growing the aecia of *Puccinia graminis* on barberry from basidiospores, and in the following January (1865) the result was duly announced.

During the year 1865 de Bary experimentally completed the life-cycle of the rye rust, *Puccinia rubigo-vera secalis* and of the oat rust, *P. coronata* (1866a). He considered that this behavior of the rusts regarding their hosts merited a new term, and consequently proposed to call species requiring a change of hosts "heteroecious parasites," and those not requiring such a change "autoecious" (1865). It was pointed out, however, that monoecious is the true opposite to heteroecious, and not autoecious. But as the term had been in use since the days of Linnaeus in an entirely different sense, and consequently was not

available, it was proposed that the terms "monoxen" and "heteroxen" be substituted. These terms and others were discussed by de Bary (1867, p. 264), who decided to retain "autoecious," and to use "metoecious" as the opposing term. Although de Bary used metoecious in his subsequent writings, the term has not been adopted by other authors.

The phrase "alternation of generations." — The phrase "alternation of generations" was first used by Steenstrup in 1842 (*l.c.*, p. 71) to apply to the alternating metamorphoses "which constitute a complete cycle" in the development of certain species of "bell-shaped polyps (Campanularia), claviform-polyps (Coryne), medusae, salpae, vorticellae, and entozoa" [cestodes and trematodes]. A few years later Hofmeister gave prominence to the phrase by contrasting stages in the life-cycle of the higher cryptogams. Much later it was pointed out by Čelakovský that there were different kinds of alternation: the homologous, which took place between generations of similar morphologic character, and the antithetic, between generations that were fundamentally unlike. The two generations in the latter case were distinguished as "protophyte," because pre-existent from the point of view of descent, and "antiphyte." These terms, which were proposed by Čelakovský in 1869, and afterward more fully elucidated (1874, 1877), correspond to the later and more familiar terms, gametophyte and sporophyte. Although the subject was elaborated by various writers, and especially by Bower,[1] the phrase continued to have uncertain application until about 1894, when Strasburger and others introduced a cytologic basis, which led to the use of the terms haploid and diploid, designated as x and $2x$ or n and $2n$.

The discovery among the rusts of an alternation of generations was made by de Bary (1863a), but without a clear conception of its full significance. It was still, as with Steenstrup and others, conceived to be of the homologous type and based on a change in form. Not only were all autoecious macrocyclic rusts considered by de Bary to possess an alternation of generations, but in his latest work (1887, p. 281) he significantly points out that there is an alternating stage even in such microcyclic forms as Endophyllum, where "there is always an intervening alternating generation," the promycelium, "though it is only a transitory state." The terms "alternation of hosts," *i.e.*, heteroecism, and "alternation of generations," should not be confused. As

[1] Bower, F. O. On antithetic as distinct from homologous alternation of generations in plants. Ann. Bot. **4** : 347–370. 1890.

used by de Bary, and by most later writers, the former term is applicable to a restricted number of species, while the latter term is applicable to all species of rusts.

The true antithetic character of the alternating generations among the rusts was first indicated by Blackman (1904), who demonstrated the origin of the binucleate condition at the base of the aecium, Sappin-Trouffy (1896) having previously shown how the reverse process of establishing the uninucleate condition takes place in the teliospore. Blackman said (*l.c.*, p. 359) that the two alternating generations are "cytologically differentiated, the sexual generation being characterized by the presence of single nuclei, the asexual by the presence of paired (conjugate) nuclei." Blackman's statement was more specifically formulated by Christman (1907b) in the words: "the gametophyte generation consists of a mycelium of uninucleated cells beginning with the sporidia and ending with the fusion of two gametes," while "the binucleated sporophytic generation has its beginning in the cell produced by the fusion of two gametes, the fusion cell."

Whatever views may be held regarding the details of a technical application, the existence of antithetic stages in the rusts is beyond dispute at the present time. The doubling of nuclei with their chromosomes and a subsequent reduction, corresponds to the definition recently formulated by Wilson (1925, p. 492), that "the process, typically illustrated by the alternation of the diploid leafy fern-plant and the haploid prothallium, is now generally designated as antithetic in contradistinction to homologous alternation in which both generations have the same number of chromosomes."

Continuity of the mycelium. — De Bary at the time he announced his belief in an alternation of generations for the rusts, drew the erroneous conclusion from his observations that the various sori of an autoecious, "aecidia-forming" species were derived from a continuous mycelium. "It is certain," he says, referring to *Uromyces fabae*, "that these [uredinia and telia] are produced by the same mycelium as the spermogonia and aecidia" (1863a, p. 76). Such a belief in the production of all spore-forms from one body of mycelium, has generally been accepted nearly up to the present time for all, except heteroecious, species. The deduction of de Bary has not, however, been verified by a rigid experimental test, and no claim is made at the present time that any macrocyclic species exists having a continuous mycelium throughout its whole life-cycle, when growing under favorable conditions for normal development (p. 98).

THE MODERN PERIOD

The apostle of the modern period for the rusts, who preached a new doctrine, based upon new conceptions and new methods, was de Bary. He was a man of the hour. The intellectual world of science was at the time seething with pronouncements of great import that were destined to affect many departments of knowledge profoundly. Pasteur was fast destroying the substructure of the ancient belief in spontaneous generation, and in this movement de Bary took a deep and active interest. Darwin had just launched the attack on that other venerable belief in the distinctiveness and immutability of species, and the echoes of the combat still ring in our ears. The broad and logical views of de Bary, supported by improved methods of demonstration, wrought a radical change in the domain of the rusts. Their autonomous nature was established, and the disquieting argument of spontaneous generation as then understood, forever banished. They were shown to have the characteristics of other fungi, although wholly parasitic. Moreover, he was the first absolutely to assert that they constitute a natural group, and to point out important biological divisions among them, calling some of them "tremelloid" and others "aecidia-bearing." It is to him that we are indebted for the basis of our present conceptions of their life-history. He indicated the relationship of the different kinds of spores and ascertained the order of their appearance. He supplied a new terminology. He pointed out the narrow limits of their parasitism, and also demonstrated that they were at the same time capable of the most astounding jumps in the selection of hosts, a fact for which he supplied the name heteroecism. And not least of all he introduced new methods of study, especially for tracing their course of development by means of controlled cultures, which are still proving of the greatest importance.

Polymorphism and the change of hosts. — The most striking feature of the new era for the rusts was undoubtedly the announcement of heteroecism, which followed almost immediately upon the discovery of a regularly recurring polymorphism. The fact that a fungus could change from one form to another of wholly unlike appearance, as the researches of de Bary indicated, was a novel idea, and that, moreover, in certain species this change coincided with a more astonishing change in habitat, brought forward views that were so alien to common thought and had been so strenuously opposed, notably by mycologists, that it is not surprising to find that there was very

slow acceptance of the new conceptions and relationships which they implied. In fact they did not become a factor to modify materially the work of observers and writers generally until well toward 1890.

Evidences of the truth of heteroecism, experimentally established by de Bary in 1864 and announced in January, 1865, were slowly and gradually accumulated. The inspiring suggestions of de Bary (1863a), independently supported by the observations of orchardists, led the Danish botanist Ørsted (1865a) to a successful result with *Gymnosporangium sabinae* in the summer of 1865. Both de Bary and Ørsted reported connections for additional species in 1866. Thereafter almost every year one to three new records were made by no less than fifteen other mycologists up to 1884. After that date a dozen or more records were sometimes reported in one year. By far the longest series of reports by a single experimenter are those of Klebahn, 1892–1924, and Arthur, 1900–1917. A full list of all reported cultures is given by Klebahn (1904a) up to the year 1904, totaling over 150 species belonging to ten genera. A list of all heteroecious species up to 1918, giving the alternate hosts, was published by Dietel (1918), numbering about 264. A list of cultures by Arthur (1921) includes a large portion of the heteroecious species known in North America, together with their alternate hosts. Omitting synonyms they number about 100.

Introduction of controlled cultures. — Studying the rusts by means of controlled cultures has proved a fertile method for securing exact knowledge of their polymorphism, parasitism and general habits. De Bary (1863a), who originated the method (*cf.* de Bary, 1887, p. 120), grew the host-plants for his cultures in pots either as small plants or seedlings, and during the initial period of one or two days covered them with bell-jars to secure the needed humidity as well as protection from stray infection. The culture period lasted ten months, from June to the next April, during which time the potted plants with similar plants uninoculated for controls were kept in the laboratory. Essentially the same methods with only slight variations were used by Ørsted (1865b), Schroeter (1875), Cornu (1882), and others, usually beginning the cultures in May. An important series of cultures, extending over a number of years, was successfully carried out by Plowright (1889, pp. 114–118) in his garden at King's Lynn, England. This garden was only a strip of land about twelve feet wide and one hundred feet long between the side of his house and a high brick wall, with a brick walk the full length. Most of the more recent experimenters, however, have grown their host-plants wholly or partly under

the protection of a greenhouse (Eriksson & Henning, 1896, pp. 367–383; Ward, 1902a; Arthur, 1902c; Klebahn, 1904a, pp. 84–97). Especially elaborate methods were devised by Eriksson.[1]

Origin of the terms "long-cycle" and "short-cycle." — The clear distinction between the two classes of rusts, which de Bary had designated as "aecidia-bearing" and "tremelloid," and the necessity of considering each species of the Uredinales as belonging to one or the other group, became more and more evident as work progressed on the rust-flora of North America in the mycologic laboratory of the Agricultural Experiment Station of Purdue University, Lafayette, Indiana. Having reached the belief that all species of rusts passed either through a cycle having aecia, telia, and usually pycnia and uredinia, or else through a cycle with only one spore-form beside pycnia, the terms "long-cycle" and " short-cycle" were adopted for convenient distinction. These terms were first utilized in print by Orton (1912), Olive (1913) and Travelbee (1915), who were assisting at the time with the rust investigations. The terms were subsequently more explicitly used to indicate that in addition to the spore-forms the mycelium in the cycle in one case was discontinuous and in the other continuous. These terms much later (Arthur & Kern, 1926a), at the suggestion of von Lagerheim, were converted into the terms macrocyclic and microcyclic, as more serviceable although having the same significance.

Predicting the kind of spores in a cycle. — The statement by de Bary, supported by all subsequent researches, that each species of rust possesses from two to five kinds of spores which appear in a definite and unvarying order, also recognized the fact that all species do not produce their full potential number of forms. A method of predicting in the majority of instances how many kinds of spores belong in a cycle, by taking into account the association of the pycnia, was first pointed out by Arthur in 1904b. A method of indicating the probable aecial host of a heteroecious rust, by observing the host of a microcyclic species whose microtelia are morphologically like the telia of the heteroecious species, was announced by Tranzschel in 1904, which has come to be known as Tranzschel's law. In one instance it has been supplemented by a chemical reaction (p. 100).

Symbols to denote spore-stages. — Knowledge relating to the number and succession of spore-stages was first utilized in systematic literature by Fuckel in 1870. He designated the three stages as

[1] In Chapter X will be found an account of still more recent culture methods.

hymeniiferus, stylosporiferus, and teleutosporiferus, terms which were not adopted by other mycologists. Karsten (1879) first used the symbols I, II, III, consistently to indicate the three stages. Fuckel (1870) had previously employed these Roman numerals interchangeably to show the order in which the stages appeared in particular species, but not for the stages themselves. To these symbols "O" for pycnia was added by Trail in 1890. The method of indicating and describing species introduced by Karsten (1879), and shortly followed by Winter (1881), has since been the standard in systematic literature. The use of "y" (Arthur, 1904b) and "S" (Hariot, 1908) for pycnia and of "IV" for basidiospores (McAlpine, 1906) has received little support. In 1901 the use of small letters, i, ii, iii (lower case), was introduced by Arthur and Holway to indicate in citing a particular specimen that the stage so designated was scantily represented.

To show the presence or absence of spore-stages Schroeter (1870) employed the device of adding syllables before or after the generic names to supply subgeneric divisions. He first used the following ten combinations: *Euuromyces*, *Hemiuromyces*, *Uromycopsis*, *Microuromyces*, *Eupuccinia*, *Hemipuccinia*, *Pucciniopsis*, *Micropuccinia*, *Heteropuccinia* and *Leptopuccinia*. In his later works he extended the terms to other genera, especially in his flora of Silesia (1889), where he added *Brachyuromyces*, *Brachypuccinia* and *Auteupuccinia*. As used by Schroeter these subgeneric terms signified (1) eu-forms, with all spore-stages and autoecious, (2) hetero-forms, with all spore-stages but heteroecious, (3) hemi-forms, with only uredinia and telia, (4) -opsis-forms, with pycnia, aecia and telia on same host, (5) micro-forms, with only telia, germination after a resting period, (6) lepto-forms, with only telia, germination without a resting period, (7) brachy-forms, like hemi-forms, but with pycnia present, and finally (8) auteu-forms, with all spore-stages but autoecious. In the later work hetero- and auteu-forms were made to be divisions of the eu-forms. The terms were found to be serviceable by other writers, and were variously extended and more or less modified in application, sometimes being raised to generic rank. They are still much used. After about 1890 Karsten's Roman symbols began to be applied in combination with the Schroeterian terminology. The system attained so much importance that the several prefixes and the one suffix have often been turned into independent adjectival words.

The most elaborate set of terms of this character was proposed by Maire (1911), and justified by him for its convenience in showing the

association of fruiting-forms for species that are "not complete," *i.e.* lacking one or more of the stages represented by the symbols O, I, II, III, the pycnia playing as important a part as any other form. They are all prefixes, *viz.*; cata-, brachy-, hypo-, opsi-, catopsi-, hemi-, micro-, endo- and pyro-. The endo-forms possess O and I only, and are represented by Endophyllum. There appears to be no provision in this plan to show whether the spore-forms required to make a specified species "complete" are either non-existent or else undiscovered. It clearly makes a vast difference whether O, I, is used to represent the endo-uredinales (*e.g.*, *Endophyllum sempervivi*), where the full life-history is known and no other spore-forms can be expected, or on the other hand used to represent an unattached species of Aecidium, which may be assumed to have in its life-cycle uredinia and telia, or possibly only telia, when these are discoverd. Again O, III, does not differ in anywise from III, when the III is potentially preceded by pycnia, as in most micro-forms, the whole life-history being known in both instances, but does differ materially from III when representing some species presumably having other spore-forms, *e.g.*, the telia of some little-known Puccinia on grass. It is in fact evident after a short examination that such systems of spore-combinations, however elaborated, can do no more than serve in particular instances, and can never be of general application. There are no natural affinities involved.

NEW DIRECTION GIVEN BY CYTOLOGY

The publication of de Bary's "Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien" in 1884, and the English version in 1887, placed the study of the rusts upon a firm and broad foundation, and gave a comprehensive treatment that has not yet been superseded. In that work de Bary said, "we are still unacquainted with the first beginnings of the hymenium" (1887, p. 278). This was true until Sappin-Trouffy (1896), under the direction of Dangeard, undertook an extensive study of the cellular structure and progressive development of the sorus in representative genera of the rusts. He studied 36 species belonging to 10 or more genera, and illustrated his work with 69 sketches, most of them quite elaborate. They were made especially effective by being partly diagrammatic. The only work of the kind at all comparable in extent or importance which has since been issued, is that by Kursanov (1915, 1922) under a similar title. A recent work by Lindfors (1924) is in the same line but less

comprehensive. A number of other investigators have made large contributions, but no single work since 1896 has embraced the study of so many and diverse genera and species. Sappin-Trouffy's work included a study of the mycelium as well as of the organs of fructification. In the behavior of the nuclei new grounds were found for the dogma of an alternation of generations. In these several works the main effort was directed toward elucidating the structure of the various kinds of sori, and the origin and utilization of the spores. The authors gave particular attention to the behavior of the nuclei, and in the discussion of results emphasized the bearing upon possible sexuality.

Although the study of developmental morphology, or what was formerly called histology, is to be considered in its bearing upon relationships as the most important part of the revelations of the microscope, yet the stronger appeal to investigators has been cytology, or the form and behavior of the cell contents, the special urge being toward an elucidation of the problem of sexuality. It is, however, to morphology that we must turn to obtain knowledge of the true and detailed structure of the reproductive organs and of their origin, without which a natural system of classification is impossible. Few investigators have made this subject a primary object of their labors. Besides the articles by Sappin-Trouffy, Kursanov, and Lindfors, mentioned above, morphologic knowledge must be sought as incidental accompaniment to cytologic investigations of certain species or small groups of species, usually of a limited range of relationships. Yet a detailed study of the comparative morphology for the different sori of many genera is needed before it will be possible to approximate a clear understanding of the fundamental features that enter into a systematic account of the rusts as a whole.

Flask-shaped pycnia and cupulate aecia were the structures that first attracted attention as embodying the features of sex organs. Pycnia were discovered by Unger (1833, p. 300), and considered by him to be a distinct kind of fungus, for which he established the genus Aecidiolum, and to which species were assigned as late as 1916 (González, p. 57). Meyen (1841, p. 143) early called attention to the close association of pycnia and aecia and believed that "we have here before us different sexes of one and the same fungus." The name of spermogonia was applied to the pycnia by Tulasne (1851, p. 377), who adopted it from the very similar structures in collemaceous lichens, where they were early believed to be of a sexual nature. He especially men-

tions *Uredo suaveolens*, *Aecidium grossulariae*, *Roestelia cancellata*, and some other species. No well-formed organs like the pycnia are to be found in any group of the true Basidiomycetes, but are common in the Ascomycetes, where organs somewhat analogous to the aecia are also found. The studies by Cornu in 1876a, Stahl[1] in 1877, and Möller in 1888 regarding sexuality in the Ascomycetes supported similar studies in the Uredinales, and led to much controversy. The sexual theory seemed very plausible for those who believed like Meyen that the pycnia and aecia constituted the whole cycle of development. The theory remained unchanged and equally plausible when the cycle was understood to be larger, and the uredinia and telia were looked upon as conidia, even if it were necessary to admit that actual sexual fertilization had ceased to take place, and an essentially sexless condition had ensued.

A new factor entered the discussion regarding sexuality when cytologic studies began. It was shown by Sappin-Trouffy (1896) that a fusion of nuclei occurs in the maturation of the teliospore, and that a reduction of chromosomes follows in the basidium. This was assumed to represent a true sexual process, comparable with the fusion of nuclei in the ascus of the Ascomycetes, and in the basidium of the Basidiomycetes. The origin of the fusion-nuclei was at the time considered unimportant, and the pycnia were left out of the question by calling them conidia.

Renewed interest was given to the subject when Blackman (1904) discovered in several instances the passage of a nucleus from one cell into an adjoining cell in the young aecium, thus inaugurating the binucleate condition. The process was interpreted as the beginning of a sexual act that had its consummation in nuclear fusion and reduction of chromosomes at the time the teliospore germinates. The buffer cells above the chains of aeciospores were viewed as degenerate trichogynes. Blackman worked with the caeomoid aecia of Phragmidium and was followed by Christman (1905a) with caeomoid aecia of *Gymnoconia interstitialis* and *Earlea speciosa* (*Phragmidium speciosum*), and cupulate aecia of the autoecious *Uromyces caladii*, and (1907a) the stylosporic aecia of *Frommea obtusa* (*Phragmidium potentillae-canadensis*). They reached comparable results as interpreted by later work. In the meantime Blackman and Fraser (1906) studied the cupulate aecia of the heteroecious *Uromyces poae* and *Puccinia poarum*, the

[1] Stahl, C. E. Beiträge zur Entwickelungsgeschichte der Flechten. Heft. 1. Ueber die geschlechtliche Fortpflanzung der Collemaceen, 55 pp. 4 pl. 1877.

caeomate aecia of the heteroecious *Melampsora rostrupii*, and the microcyclic species *Uromyces ficariae*, *Puccinia adoxae* and *P. malvacearum*. Olive (1908a) soon after reported studies on the stylosporic aecia of *Triphragmium ulmariae* and the microcyclic *Puccinia transformans*. These several investigations together with that of Maire (1900) on Endophyllum, covering a wide range of Schroeterian forms, clearly brought out the fact that a fusion of cells in pairs takes place at the base of the hymenium in the several forms of aecia as well as in various forms of microtelia, or else at some indefinite distance preceding this point. In this way the binucleate condition characteristic of the sporophytic stage is initiated. In the discussion of their discoveries by the several authors, and subsequently, it has been maintained that the fusion of cells by pairs is to be interpreted as in some manner representing the beginning of a sex act, which finds its completion in the teliospore. The theory of a rudimentary trichogyne was finally discarded.

In the prosecution of the fascinating problem of sex in the rusts much cytologic information has come to light. The beginning of cytology for the rusts probably dates back only to Schmitz (1880, p. 195), who discovered conjugate nuclei in the mycelium and urediniospores of *Coleosporium campanulae*. Later, nuclei were seen by Rosen (1892) in the mycelium, pycniospores, aeciospores, urediniospores and teliospores, working with *Uromyces pisi* and *Puccinia asarina*, and some details of their structure and behavior ascertained. Poirault and Raciborsky (1895) claim the prior distinction of seeing the chromosomes, and something of the part they take in the fusion and division of the teliosporic nucleus. To them we can trace the expression, "conjugate nuclei."

The behavior of the nuclei in many species is figured and described by Sappin-Trouffy (1896), and especially in detail for teliospores of *Coleosporium sonchi* (*l.c.*, pp. 141–148). Juel (1898) illustrates a somewhat different manner of nuclear behavior for teliospores of *Coleosporium campanulae*. Especially clear detail has been shown by Holden and Harper (1903) for teliospores of *Coleosporium solidaginis* (Fig. 61) erroneously given as "*C. sonchi-arvensis*." Other investigators, among whom may be named Maire, Blackman, Olive, Moreau, Arnaud, Kursanov and Dodge, added in turn various details regarding the nucleus and its changes. Lastly in the list of those to be mentioned, Colley (1918) and especially Lindfors (1924) figure and describe clearly and minutely the transformations that take place in the nucleus

beginning with the resting state, and passing through the prophase, formation of spindle, changes in position of the chromatin and appearance of chromosomes, movement of nucleoli, the metaphase, then through the several adjustments during the anaphase, back to the resting state. Although knowledge regarding the nucleus and its behavior has been much advanced, still no one has yet addressed himself to the problem of an independent, comprehensive study. The minuteness of the nuclei in rusts presents special difficulties, and calls for refined technic.

TERMINOLOGY OF THE RUSTS

Many technical terms employed to give increased accuracy in descriptions of the rusts have been adapted from other groups of fungi and applied to homologous structures, or what were assumed to be such. Other terms have arisen to meet the special requirements presented by the rusts, and have not, or only rarely, been used outside the group. That exclusive terms are needed comes from the fact that the Uredinales are *sui generis* in some respects, particularly as to their organs of reproduction.

Terms applied to the vegetative body. — The word "byssus" is of ancient origin and in olden times was applied to a fine quality of flax. It was given to any growth of loose fungous threads by the early mycologists, and was erected into a genus by Micheli (1729). It continued as a genus until 1847, although also used in a general sense. The term "hypha," taken from the weaving industry, passed through the same stages as the preceding, being made a genus in 1822 by Persoon, but early became the recognized elemental portion of the mycelium. The term "mycelium" is the Latin form of an early Greek word applied to fungi in general, and more especially so to the larger forms. It was first used in its technical sense by Trattinick in 1809 for the solid body of the fleshy fungi. Its first application to the rusts was by Léveillé (1839, p. 10). Corda who independently discovered and figured the mycelium of rusts in 1839, applied no special name to it until later (1840, p. 9) when he employed the term "hypothallus."

Germ-tubes and promycelia. — When spores germinate the hyphae which arise from them are known as "germ-tubes" or "promycelia." Usage has restricted the term germ-tube largely to the hyphae that normally grow indefinitely and may be branched, as those from aeciospores and urediniospores (Fig. 41), while promycelium is used

for hyphae that issue from a teliospore or microteliospore and have a definite growth, terminating in a basidium. The terms in both cases are generally understood to apply to the first growth from the spore, this growth being essentially a single cell, rarely becoming septate until changed to an endophytic mycelium or to a basidium. Sometimes promycelium is made a synonymous term with basidium.

Fig. 41. — Contorted and branched germ-tube of *Peridermium pini*. (After the Tulasnes, 1847.)

The term "promycelium" was introduced into the literature of the rusts by Tulasne (1853), to indicate a hyphal growth from the spores of aecia, uredinia and telia introductory to the formation of the endophytic mycelium, and that it perished upon serving its purpose. At this time Tulasne had not seen a basidium arising from the promycelium of a teliospore, and did not know that the outgrowth of a teliospore differed in any respect from that of other rust spores. The germination of a column of teliospores of *Cronartium asclepiadeum* was early figured by Unger (1833), but he mistook the basidia for "sporidia," and the basidiospores for "sporidiola," which he believed were formed within the "sporidia" and escaped through ruptures (Fig. 42).

Van Tieghem (1893) proposed that the teliospore be called a probasidium, inasmuch as the latter "acts not as a spore, since all spores produce a thallus, but as a temporary intermission in the development, a sort of encystment of the basidium." This usage was adopted by Patouillard (1900) and Hariot (1908), and is still employed by a few other writers.

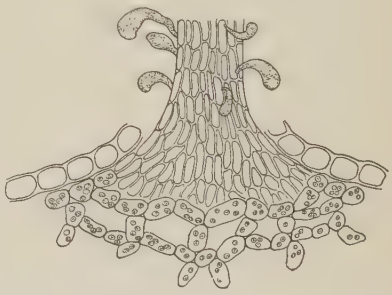


Fig. 42. — Lower part of a telium of *Cronartium asclepiadeum* with germinating teliospores, as seen by Unger: the young promycelia contain vacuolated protoplasm; Unger mistook the vacuoles for basidiospores. (After Unger, 1833.)

Terms applied to the reproductive structures. — The fruiting organs as individual structures have been variously denominated. A sorus of the general appearance of that in the genus Aecidium was first called a "theca" or "cespitosus" by Persoon (1794). The latter term was employed by him in his chief systematic work of 1801, and

there extended to the other forms of sori, in which usage he was followed in part by Rebentisch (1804). Most early authors however applied no special term to the organ of fructification. In descriptive writing it was not infrequently called a "sporangium."

When de Bary began his studies, being struck by the similarity in structure between aecial cups and certain reproductive bodies among the Pyrenomycetes, he utilized the name "perithecium" (1853, p. 72), originally proposed by Nees von Esenbeck in 1816 (*l.c.*, p. 275) for other kinds of fungi. Later "merenchyma-body" was substituted by de Bary (1866b, p. 185) for perithecium. These terms were dropped in his work of 1884 (*l.c.*, p. 296), and no others supplied.

The term "sorus" now in common use, was introduced by the Tulasne brothers in 1847 (*l.c.*, p. 43), and at once adopted by most mycological authors, except those of Germany who did not begin to employ it until about 1890. For a time a few authors used "acervulus" or "acervus" while most German authors used "sporenlager."

Sorus had been, and still is, the name employed for fruiting parts of ferns, lichens and some fungi. It was not uniformly applied to all the fruiting organs of the rusts and exactly defined until 1905 (Arthur, 1905b).

The word "stroma" has been employed in a number of ways, and so far as the rusts are concerned has never attained the position of a fixed technical term. It was introduced into mycologic literature by Persoon (1794), who used it in making subdivisions of the genus Sphaeria. In its application to the Ascomycetes the word has generally denoted the tissue-like substance in which the spore-structures are imbedded. In connection with the rusts it was employed by Nees von Esenbeck (1816, p. 275) for the base or under part of a sorus, the cushion of hyphae on which the sorus rested. This part has also been called "sporodochium" by Link (1825), and "clinode" (clinium) by Léveillé (1846). The former term, somewhat loosely applied, was still in use in 1889 (Plowright, 1889; Bolley, 1889b) and even later.

The felting of hyphae often seen about an aecium was designated as "pseudostroma" by de Bary (1853, p. 77). In the "North American Flora" (Arthur, 1907–27) the term "stroma" has been applied to the modified paraphyses surrounding certain subepidermal sori.

The stroma as an envelope of the reproductive parts was for a time considered of much systematic importance. Duby (1830) used it to distinguish the Uredineae, with which he placed the Tubercularieae and Melanconieae. A "stromatic series," which had the stroma for

its fundamental element, was separated from the Ascomycetes by Zukal (1889), and treated as an offshoot of the Uredinales. Other authors have attached more or less importance to the stroma as an indication of relationship, but more recently its value in this respect has not been considered important.

A mature sorus consists of three main parts: the spores, the basal layer from which the spores arise, and the protecting envelope. The envelope when of a membranous nature was called a "peridium" by Persoon (1796), a term which has been generally accepted, and is still in use. Link (1809) interpreted the peridium as a part of the host, a kind of indusium, and not a part of the fungus, and in 1825 called it a "pseudoperidium." This substitute term was adopted by Fries, Rudolphi, and Unger, and has had considerable vogue by other authors even down to the present time.

When the sterile elements of a sorus are not united into a membranous structure, but are independently produced, either interspersed with the spores, as in the uredinia of Melampsora (Fig. 8 *B*), or as a fringe about the margin of the sorus, as common in certain forms of pycnia (Fig. 11 *c*) and in most uredinia, and less so in aecia (Fig. 8 *A*) and telia, they are called "paraphyses." The term was applied to sterile parts of various fungi, lichens, etc., by Montagne (1841) and transferred to the rusts by Tulasne brothers in 1847. Léveillé at the same time (1847) proposed for these the term "cystidia" ("cystide"), because of their similarity to the sterile cells in the hymenium of the fleshy fungi. The "cysts" about the telial heads of species of Ravenelia (Figs. 25 *s* and 43 *B*) are considered (Dietel, 1894) to be a portion of the pedicels beneath the individual spores, which contains a hygroscopic substance often capable of absorbing water until the cyst bursts. The colorless "cysts" on the pedicels of species of Uromycladium (Fig. 43 *A*) are clearly of the same nature, but are only slightly hygroscopic. Both forms have the same significance in the life of the rust as the hygroscopic portion of the

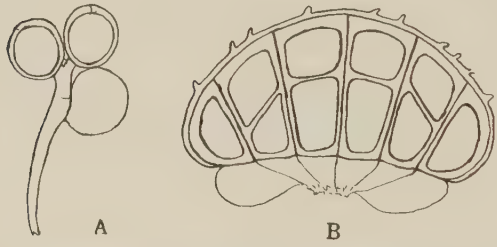


FIG. 43. — Teliospore-heads: *A Uromycladium maritimum*, an Australian rust on Acacia, with two teliospores and a very thin-walled cyst; *B Ravenelia indigoferae* in vertical section, marginal spores one-celled, central spores two-celled, cysts beneath. (*A* after McAlpine, 1906; *B* in part after Dietel, Beih. Bot. Centr. II. **20** : pl. 6.)

spore-wall and pedicels in Uropyxis, Phragmidium (Fig. 25*f*, *n*), and other genera.

We need not trouble ourselves about the exact propriety (de Bary 1887, p. 276; Gäumann, 1928, p. 554), in choosing between the two forms of the term, paraphyses (growing beside) and periphyses (growing around), for taken either etymologically or morphologically they are equally applicable for the rusts. De Bary (1887, p. 275) recognized the homology of the peridium and the paraphyses by calling the circle of peripheral paraphyses a "paraphyses-envelope."

After dehiscence of the mature sorus, when no peridium is associated with it, the term "naked" is applied. The term dates from the time of de Bary (1863b, p. 633), who applied it to sori "lacking a peridium." This has been, and still is, the general usage, although not wholly consistent, for a sorus is said to be "naked," even if it possesses paraphyses, either few or many, and the paraphyses may form as close an envelope as a peridium.

The hymenium, which is the sporiferous layer in the sorus, derives its name from early usage for such a layer in fungi in general, but more especially in the Ascomycetes. The application does not necessarily involve the idea of sexuality, although the name is derived from the Greek word that was used both for a membrane and for the god of marriage, Hymen.

The hymenium is the spore-bearing layer, and is composed of the "basal cells," and the first fertile and sterile elements that arise from them. In aecia, uredinia and telia the basal cells are short and comparatively broad, and support the spores or at first the spore initials. In early usage the basal cells were called "basidia" (de Bary, 1887, p. 274) for the same reasons, but as a technical term the word basidium is now differently applied. The basal cells in the aecium and microtelium are usually the product of cell fusion and have frequently been designated as "fusion cells," although it is better to consider the fusion cells as passing over into basal cells after their union. The hymenium of the higher Basidiomycetes is to be considered in some respects the homolog of the hymenium in the sori of the rusts.

The word "spore" is of Greek origin, denoting a seed or germ. It came into botanical use when Hedwig in 1787 applied it to the spores of mosses. In 1796 it was used for the spores of rusts by Persoon (1796, p. 98) and later (1799, p. 23) he substituted the diminutive form of the word, "sporula." The idea introduced by Hooke, that the spores of the rusts were to be considered seed-pods, inside of

which were exceedingly minute reproductive bodies (p. 36), led to the use by DeCandolle of "pericarp" for the spore in his earlier writings and of "capsule" as a technical term in his later general writings and in his Flore Française (1805). This terminology found supporters for nearly a half century even among the best mycologists, such as the Tulasne brothers (1847). In this connection the term "grains" or "spores" designated the granules within the capsules, which were the bodies supposed to effect reproduction. Link in 1825 introduced another diminutive form, "sporidium," for the various rust spores. Recent authors usually confine this term to the basidiospore. For the most part, however, authors used, and are still using, the word spore as a general term for all sorts of reproductive bodies among the rusts, whether unicellular or multicellular. Vuillemin (1893b) defines a spore to be "a unicellular or paucicellular organ destined to be isolated from the vegetative body to conserve or propagate the plant."

There are two general forms of spores, pedicellate and catenulate. The pedicellate form results when the lower cell formed by the spore initial loses the power of further division and is transformed into a pedicel supporting a one- to many-celled spore, while the catenulate form results when a lineal succession of cells is produced by the spore initial without a pedicel.

In 1832 Fries (*l.c.*, p. 263) proposed the term "conidia" to serve among the fungi as the equivalent of gonidia as applied to the lichens by Wallroth in 1825. Although de Bary (1887, p. 131) gave the weight of his authority in favor of adopting gonidia in place of Fries' term, as older and more suitable, and wrote about "uredogonidia" and "teleutogonidia" (1887, p. 281), yet all modern writers adhere to conidia, and use it, as a rule, for almost any kind of spore produced asexually, especially when produced externally.

It was the Tulasne brothers (1847) who first introduced a definite method of discriminating between the several kinds of spores among the rusts by classifying the sori into (1) spermogonia, producing spermatia, and (2) "fruits," the latter being of two kinds, one producing stylospores and the other "perfect" spores (*sporae perfectiores*). The "perfect" or true spores were those that germinate with a limited promycelim, *e.g.*, teliospores of Phragmidium, Puccinia, Uromyces, etc., and stylospores were the common form of urediniospores. At that time a rust species was considered to have only urediniospores and teliospores. These terms were employed for a time by de Bary. When he ascertained by means of cultures that aecia by their nature and

general characters were to be associated with the uredinia, and were consequently stylospores in the Tulasne sense, he at first distinguished the two kinds as the "stylospores of Aecidium" (1863a, p. 76) and "stylospores of Uredo" (*l.c.*, p. 77), soon changing to "stylospores-Aecidium" and "stylospores-Uredo" (*l.c.*, p. 84). A year or two later, finding these terms too clumsy, he introduced "aecidiospore" and "uredospore" with the following justification: "In reference to the use of technical terms it may be observed that the words Aecidium and Uredo originally were genus names, because they were considered only to represent special genera. Now the same are rightly employed to designate particular organs" (1865, p. 17). This reasoning was reiterated by Winter (1881, p. 132). At the same time de Bary (1865, p. 16) proposed in place of Tulasne's "true spore" in the narrow sense, the term teleutospore, because it "appears at the end of the development of the species."

This reform in terminology seemed quite sufficient in the days when the rusts were interpreted by the behavior of *Puccinia graminis* and species which could be considered similar. It was not long, however, before the need of greater discrimination arose. This was easily met by following the direction at first indicated by de Bary; and the literature became laden with roesteliospore, caeomospore, peridermiospore, epiteospore, etc., the only limit being the number of present or past form-genera. Sometimes even true genera were utilized.

The attempts to discriminate between the different kinds of reproductive bodies had so far been largely based upon the assumption that each of the then known genera, many of which we now call form-genera, possessed a peculiar kind of spore. An entirely different method was employed in 1905 (Arthur, 1905b) when the five fruiting structures occurring among the rusts, as indicated by de Bary, were given names independent of the genera involved. They are pycnia, aecia, uredinia and telia, and the names of spores are derived from them, *e.g.*, pycniospore, aeciospore, etc. These terms were not explicitly defined and their application suitably illustrated until two decades later (Arthur & Kern, 1926a).

A few special forms of spores have acquired technical names that are useful. It was early noticed (Tulasne, 1854b) that in the telia of various species of Puccinia there occurred one-celled spores that were otherwise like the two-celled spores. These were called "mesospores," being interpreted as intermediate in point of development between simple and compound forms (Winter, 1881, p. 133). Later Sorauer

(1886, p. 213) considered them to be intermediate between urediniospores and teliospores, but Dietel (1887, p. 56) showed that this could not be the true relationship, as they occur plentifully in microcyclic species, *e.g.*, *Puccinia heterospora.*

The term "mesospore" was applied by Dietel (1889, p. 179) to a resting form of urediniospore observed in *Puccinia vexans* from midwestern North America, but some years later Carleton (1901, p. 250) proposed the term "amphispore" for the same kind of spore and occurring in the same species of rust, a term that has since prevailed. Carleton had germinated and cultured such spores and based his name upon their physiologically intermediate character in some respects between urediniospores and teliospores.

A small, smooth and thin-walled spore found associated with urediniospores and teliospores, chiefly with the former, in some species of the Australian genus Uromycladium (Fig. 44) has been called a "mesospore" by McAlpine (1896; Sydow, 1912–15). Its significance is unknown.

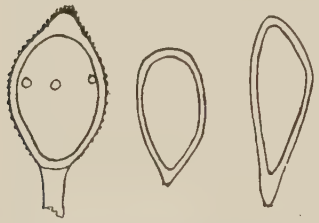


FIG. 44. — A urediniospore and two "mesospores" of *Uromycladium maritimum.* (After McAlpine, 1896.)

The spores which are the direct product of the basidium were called "sporidia" by Tulasne (1853), and have often been so called by subsequent authors. The term "promycelial spore" was used by Plowright (1889) and McAlpine (1906). "Sporidiolum," a diminutive form of sporidium, was used by De Toni (1888) in Saccardo's Sylloge Fungorum, and has been favored by many later writers. Since the rusts were classified as a part of the Basidiomycetes by Brefeld (1889) and Van Tieghem (1893) the designation basidiospore has usually been accepted as a suitable term.

PHYSIOLOGY AND SPECIALIZATION

Not much exact physiologic knowledge of the rusts antedates the beginning of the present century. Experimental methods had first to be developed, and they may be said to have originated with de Bary when he began studying the rusts by means of cultures. In his memoir before the French Academy (1863a) a number of direct physiologic experiments are recorded. He describes the behavior of the germinating basidiospore when on the surface of the host-plant, its entrance into the host and subsequent development. He tried to determine if light were the controlling factor in the unequal distribution of sori on

the two surfaces of a leaf. He experimented with *Uromyces fabae* on the broad bean (*Vicia faba*), illuminating the upper surface of some plants and the lower surface of others, and securing positive results (*l.c.*, p. 98). He also studied the effect of a humid atmosphere to increase the abundance of sori (*l.c.*, p. 97). He generalized that doubtless all kinds of rust spores require essentially the same conditions of temperature, moisture, etc., for their germination, but that immersion in water was detrimental. Naturally, many isolated observations were recorded subsequent to de Bary's initial experiments, but all that require mention which antedate the present century are noted in the chapters that follow.

That the rusts can be germinated and possibly grown saprophytically in spite of their strong parasitism, was an opinion that Brefeld (1888) tried to demonstrate experimentally, as did Carleton also (1903), but without success. Other attempts have been made in more recent years but wholly in vain up to the present time (p. 210).

The important topic of specialization was first experimentally developed by Eriksson (1894) and Carleton (1899), who carried on extensive studies simultaneously, but work by Eriksson was published earlier and longer continued. The development of the subject has been so recent that the historical features are embodied with others in a special chapter which follows.

TERATOLOGY AND PATHOLOGY

Variations from the normal course of development were observed by earlier as well as later observers. So far as direct study of abnormalities of the fungus are concerned it has been confined to the germination of the spores, the behavior of the resulting germ-tube, and of the basidium and its spores, as these are the only parts that are freely exposed and grow independently of the host.

Malnutrition. — That the spores usually do not grow in the customary manner when wholly immersed in water has been a common observation. This was especially remarked by de Bary (1863a). Figures of the abnormal development in germinating teliospores during the formation of the basidia were drawn by the Tulasnes (1847, 1854b), and by many authors subsequently. It is a curious comment that no author up to the present time has treated the variations from normal development as in anywise bordering upon a pathologic condition. Indeed, quite the opposite is not infrequently the case. Carleton (1893) gives figures and discusses the deviations in teliosporic growth

of a number of species under the caption "a new method of producing sporidiola," and concludes that "this process of germination may prove to be of importance in classification."

Teratology. — The unusual forms of spores have attracted the attention of numerous observers, ever since drawings from the microscope have been made. Usually they are treated as simple deviations of no special significance, but occasionally are considered to show evolutionary tendency.

A race of *Puccinia rubigo-vera* on Bromus, having many of its teliospores divided by transverse and vertical partitions into three to seven cells, was described by Trelease (1885) under the name of *P. tomipara* (Fig. 147). A large series of abnormal teliosporic forms was illustrated by Warren (1898), Hume (1899), and McAlpine (1906), taken from the genus Puccinia. Although the several authors have drawn some inferences regarding relationships, yet such malformations doubtless have little or no significance as evolutionary factors.

The diseased host. — After the age-long controversy regarding the relation of the rusts to disease in plants had been settled definitely by de Bary (1853) attention was naturally turned to the varied changes which the parasite effected in the host. One of the most conspicuous examples is the production of clustered adventitious branches, known from early times as witches' brooms. De Bary described the form on *Abies pectinata*, caused by *Aecidium elatinum* (1867), stating that he had seen one such growth between six and seven decimeters high and sixteen years old. He traced the mycelium through the diseased tissues, and also showed that a similar condition existed in other perennial species. The swellings and distortions in trees naturally attracted attention first. Among the earliest illustrations of rusts are the galls on Crataegus (Fig. 34) and the swellings on Juniperus (Fig. 36), both due to *Gymnosporangium clavariaeforme*. Although much attention was given to the effect of the rust on the host little or no progress was made prior to the beginning of the present century in determining the conditions under which the rust flourished. Even the anatomical examination of the host was rarely attempted (Fentzling, 1892; Hartmann, 1892).

CONTROL OF RUST AS AN ECONOMIC PROBLEM

The interest of the cultivator and economist centers in the action of the parasite upon the host, whether it produces structural changes or diverts nutrition. Two authors produced handbooks during this ini-

tial period, which served economic ends and also had a great influence in promoting scientific study and popularizing its results. Kühn (1858) devoted twenty-three pages of his treatise on the "Diseases of cultivated plants" to an excellent résumé of the rusts as then known, and Hartig (1874) summed up the knowledge of rusts in relation to trees. Both works passed through a number of editions with much augmentation, and were translated from the German into other languages.

The economic aspect has been foremost in nearly all writings pertaining to the rusts from the earliest up to recent times, and still largely prevails. The cultivator's point of view was the only one known to the ancients, and all our knowledge prior to a century and a half ago came through that channel. To such an urge we are indebted for the splendid researches of Tulasne and de Bary, and of most other important contributors to scientific uredinology. The main ostensible reason for supporting scientific inquiry at the present time is its economic bearing, and most writers, even of highly technical papers, feel the need of meeting the popular demand in a few words by way of a suitable liason. "It is said the students of Aristotle and of Theophrastus became objects of ridicule with some of the literaries, poets, satirists of the time, because of their going about the country picking up and curiously peering into the least little things of nature, such as were of no possible use. And one may not attribute to antiquity alone these prejudices against philosophic nature study; for they rule the mind of untold millions even now. Antiquity, in this phase of it, is with us still."[1]

The present volume has been arranged to develop a logical sequence of topics beginning with the recognition of the objects of inquiry and ending with the application of the knowledge to human welfare. If it had been arranged historically a nearly reverse order would have been required. Ancient writings refer to rusts only as injury to crops and in connection with means devised for crop protection. Many remedies are given by the Latin writers. Some of them were wholly fantastic, others like sticking branches of laurel about the field merely superstitious and useless, while others like burning the old straw and selection of ground not over moist were doubtless helpful. The intervention of priests has been referred to earlier in this chapter (p. 32).

During the latter part of the eighteenth century and extending into the following century there was much agitation against the barberry bush and laws were passed for its destruction both in northern Europe

[1] *Cf.* Greene, Landmarks of botanical history, 1909. p. 61.

and the United States. But the basis of more complete knowledge was required to make them effective. The same remark will apply to the cultural methods then in use, as may be illustrated by an excerpt from the diary of George Washington.[1] In an entry made at his Mount Vernon farm, July 25, 1768, he says: "From the most accurate experiments I could make this year upon wheat seized with the rust before it is fully formed and beginning to harden, it appears to be a matter of very little consequence whether it is cut down so soon as it is seized with this distemper or suffered to stand, for in either case the grain perishes and has little or no flour in it. That indeed which is suffered to stand may gain a little, and but a little, in respect to the grain, and the other in respect to the straw, so that I think it is nearly equal which of the two methods is followed."

Modern methods of controlling the rusts are treated in a subsequent chapter. The three lines of attack that have proved especially serviceable are securing resistant varieties, destruction of alternate hosts, and improved methods of culture.

[1] The diaries of George Washington. **1** : 281. 1925.

CHAPTER III

DEVELOPMENT AND CLASSIFICATION

Ontogenetic development: fundamental features of rusts, mycelium, sori; aecial and telial characters; life-cycles; discussion of sexuality; heredity; heterothallism; origin and explanation of heteroecism.

Phylogenetic development: the early period; the protistan, algal, phycomycetous, ascomycetous and basidiomycetous theories; summary of theories; the late period; progressive and retrogressive development; effect of parasitism; omission of spore-stages; shortening of life-cycle; correlation.

Classification: definition of species; influence of host and of correlation; successive prominence of pycnia, dimorphism, and telia; biologic characters; nomenclature; taxonomy.

ONTOGENETIC DEVELOPMENT

In order to attain conceptions which will lead logically to a consideration of the phylogeny and classification of a group of organisms it is well to have a definite and comprehensive knowledge of the structure and inter-relations of the members of the group. In Chapters I and II certain general and historical aspects of the rusts have been presented. A more detailed discussion of some points is necessary in order to establish a full and clear understanding of the subject.

Fundamental features of the rusts. — To summarize briefly numerous concepts already presented the following statement (Arthur & Kern, 1926a) is now made regarding the fundamental structure and ontogenetic development of the plant rusts.

All rusts possess a vegetative body (mycelium), from which arise the fruiting structures (sori).

The vegetative body is macrocyclic (long-cycle), consisting of two unlike and discontinuous generations, or microcyclic (short-cycle), consisting of one continuous generation.

The fruiting structures, the sori, contain spores that are either ineffective (having no power to bring about infection), or effective (having power to bring about infection).

The sori with ineffective spores (pycnia) are present or absent in both macrocyclic and microcyclic rusts.

The sori with effective spores (*a*) in a macrocyclic rust are the two essential forms, aecia and telia, with the supplementary, interme-

diate, repeating form, uredinia, and (*b*) in a microcyclic rust the one form, microtelia, which so closely resembles either aecia or telia that one or the other of these terms is customarily used for it.

Importance of the mycelium. — There are some important differences between the idea of rusts embodied in the preceding outline and the ideas currently entertained. It is here maintained that the rusts have a vegetative body that holds such a prominent place in their development that it requires adequate consideration. In all rusts the vegetative or mycelial body has an essentially gametophytic organization in its first period of existence. In many kinds of rusts a second stage occurs when there is the production of a mycelial body of an essentially sporophytic nature. All species possessing both stages of the mycelium in the life-cycle are classed as macrocyclic. All species possessing only the first stage of the mycelium, the second stage being reduced nearly or quite to zero, are microcyclic.

Nature of the sori. — The fruiting structures of the rusts are all of the same general structural character, being sori with a sporiferous hymenium more or less inclosed and protected by accessory growth of the fungus or the host.

The pycnia are apparently of primitively sexual nature. They occur only in the gametophytic[1] generation.

The other three forms, in a macrocyclic rust, aecia, uredinia and telia, are of a conidial nature, and are active in the propagation and multiplication of the species. They are distinguished by their histologic development and their position and service in the life-cycle.

The aecia are initiated by the gametophytic mycelium, but the aeciospores are sporophytic, and continue the life of the rust by forming a sporophytic mycelium.

The uredinia are borne on the sporophytic mycelium, and the urediniospores continue the life of the rust by forming a sporophytic mycelium in the same manner as the aeciospores.

The telia like the uredinia are borne on the sporophytic mycelium and the teliospores continue the life of the rust by forming basidia with aerial basidiospores and through these producing a gametophytic mycelium.

The one form of sorus, besides the pycnium, occurring in a microcyclic rust, the microtelium, is borne on the gametophytic mycelium, and the microteliospores continue the life of the rust in the same manner as

[1] For use of the terms gametophytic and sporophytic see Chapter I, p. 2.

teliospores, through the intervention of basidia and basidiospores. The above statement regarding the sori is summarized in the accompanying table.

TABLE 1 — SORI OF THE UREDINALES

Cycle	Name	Origin of Sorus	Nature of Spore	Continuation of Cycle
macrocyclic	pycnium	gametophytic	(sexual ?)	None
	aecium	gametophytic	asexual	Initiates a sporophytic mycelium.
	uredinium	sporophytic	asexual	Continues the sporophytic mycelium.
	telium	sporophytic	asexual	Initiates a gametophytic mycelium by means of a basidiospore.
microcyclic	pycnium	gametophytic	(sexual ?)	None.
	microtelium	gametophytic	asexual	Initiates a gametophytic mycelium by means of a basidiospore.

LIFE-CYCLES "WITH AND WITHOUT AECIA." — The present method of dividing the cycle of development in the rusts into two generations or stages, requiring the terms macrocyclic and microcyclic for the two groups, is the logical result of a comprehensive inquiry into de Bary's suggestion (1884) of "tremelloid" and "aecidia-bearing" groups (*l.c.*, p. 135). It is found that all rusts, whatever their exterior aspect, pass through a life-cycle with aecia or a life-cycle apparently without aecia. We may assume, as did de Bary (1887, p. 285), and with even more substantial reasons, that the "tremelloid" [microcyclic] forms are "descendents of aecidia-forming [macrocyclic] species and homologous with certain segments of their development."

AECIA AND TELIA ESSENTIAL IN MACROCYCLIC SPECIES. — The two forms of sori that are chiefly concerned in the continued life of macrocyclic species are the aecia and telia. The aecia in their highest development have to do with the pairing of nuclei together with their chromosomes, while the telia are associated with their fusion and reduction. The processes of cell fusion and of maturation take place in macrocyclic forms in connection with distinct sori, and are separated by a growth of sporophytic mycelium. The pycnia have heretofore been considered to be functionless, or possibly to exercise an obscure physiological action of "maleness" (Dodge, 1924c), but are now known to have some direct action in the formation of aecia (Craigie, 1927b). The uredinia serve

conidially to multiply the reproductive capacity of the rust, and their spores act in a similar manner to the acciospores. Their absence, as occurs in many species, only restricts distribution of the species without in any degree affecting individual continuity.

Aecial and telial characters in microcyclic species. — The only form of sorus essential to the continued life of microcyclic species is the microtelium. The one other form that may occur, the pycnium, arises in the same way and has the same significance as in macrocyclic species.

In microcyclic species the two processes, cell fusion and maturation, are so closely juxtaposed that they take place in connection with a single sorus, the microtelium. This sorus, therefore, possesses both aecial and telial characters, as it initiates the sporophytic stage in the hymenium and closes it in the matured spore, without the intervention of mycelium. The microtelium may consequently be said to represent a telescoping of aecia and telia with elimination of interposed mycelium.

The condition, found in certain species of rusts, in which only uninucleate cells occur throughout the whole life-cycle, much discussed in recent years, is to be considered aberrant or abnormal, and probably as arising from extreme degeneration.

Interpretation of the life-cycle. — Many writers (Maire, 1911; Mordvilko, 1925; Gäumann, 1926, 1928) speak of incomplete cycles, meaning thereby that some of the five typical forms of spores are omitted in the cycle of development. Such an expression is founded on the assumption that all rusts fundamentally have the same length of life-cycle with a uniform succession of spores, unless from degeneracy, unfavorable growth or other conditions, some of the spore-forms are omitted. From such a conception has arisen the use of symbols in combination to indicate complete and incomplete cycles (p. 55). If, however, a cycle is defined as that interval in the ontogenetic development of a species extending from the basidiospore through to the next production of basidiospores, or from any other fixed point round to the same point again, it is seen that many species may fail to produce one or more of the five possible spore-forms, and yet have complete life-cycles. It is the continuity of life that is involved in the term life-cycle, not the mode of its expression.

Limitation of the gametophytic and sporophytic phases. — It is possible to state definitely the limits of each of the two antithetic phases in the life-cycle, both in macrocyclic and microcyclic forms in terms of their morphology.

The gametophytic phase of the rusts (Fig. 3) begins with the basidium and ends with the aecial or microtelial primordium. It includes in both macrocyclic and microcyclic species the basidium with its two or four cells, the basidiospores, the mycelium which ensues from the germination of the basidiospores, the pycnia, the pycniospores, and the primordia of the aecia in macrocyclic species and of the microtelia in microcyclic species.

The sporophytic phase begins with the aecial or with the microtelial hymenium and ends in the promycelium of the teliospore or microteliospore. It includes in macrocyclic species (Fig. 3) the aecia, except in their early primordial state, the uredinia and the telia, together with their spores, intercalary cells, pedicels, peridial cells and paraphyses, and the mycelium or promycelium which ensues from their germination; while in microcyclic species (Fig. 4) it includes the microtelia, except in their early primordial state, the microteliospores and their promycelia.

In the usual expression of both macrocyclic and microcyclic species the gametophytic phase may be simplified by partial or complete omission of the pycnia, and in macrocyclic species the sporophytic phase may also be simplified by the non-appearance of the uredinia, or it may be much augmented by the multiplication of uredinial generations, sometimes to an indefinite extent. Occasionally both aecia and uredinia are omitted during a portion of the season's growth (p. 97).

Discussion of sexuality. — Some form of sexuality appears to be universal, or nearly so, among all classes of organisms, whether animal or plant. In speaking of sexuality in this general way we may define it to consist of the union of two distinct and usually more or less distantly related masses of protoplasm, with their nuclei, chromosomes and whatever else constitutes the energizing factors of the living cell, followed by a constitutional reorganization. To follow the visible course of the sexual act, attention is fixed, so far as possible, first upon the fusion of the two elements or gametes and then upon the union of the nuclei and their reorganization.

In the highest expression of the sexual process the contents of the male element, or at least the nucleus, passes over into the (generally much larger) female element, where the two nuclei fuse at once or after the lapse of a period during which more or less growth intervenes. The two conjugating elements are male and female gametes. However, as Lotsy (1907, p. 424), says, "the essence of the sexual process does not lie in the union of two sex organs, but in the union of two nuclei."

The subject of sexuality among the rusts has been prominent for nearly a century, and especially since Meyen fixed upon the pycnia and aecia as male and female organs (p. 58). Nevertheless, no process of sexuality embodying such a high type as just indicated has yet been found in any species of the rusts, although the pycnia have from first to last maintained their reputation as male organs, and correspond to such in details of gross and minute structure and in the time and place of their appearance.

Although investigators have not been able to discover a female organ as a counterpart to the male organ represented by the pycnium yet there is almost general agreement that sexual fertilization does exist in the rusts, and that a sexual act is present even if its original potency and importance are reduced. At least we may safely say with Harper (1905, p. 87) that "in the rusts we have sexual reproduction by vegetative fertilization." One evidence of the presence of sexuality is found in the uninucleate condition of the gametophyte and the binucleate condition of the sporophyte, which are really haploid and diploid phases and, therefore, correspond to similar conditions in the two similar phases of many other groups of plants. In typical macrocyclic species, like *Puccinia graminis*, the alternation of uninucleate and binucleate phases coincides with morphologic changes, as already noted (p. 74), and also in many cases with certain physiologic appearances of increased vigor following the production of aecia (Arthur, 1903b). We may assume that such species as *Puccinia graminis* represent an early primitive condition of all rusts, at least in relation to their nuclear behavior. It is a fairly accurate statement to say that in rusts of all sorts the sexual process begins with the fusion of cells during or preceding the formation of the aecium, or of the microtelium, thus instituting a dikaryon,[1] and is consummated with the maturation of the teliospore or microteliospore. The fusing cells act in the place of gametes, and may be so called.

In cases where the beginning of the binucleate condition does not synchronize with the hymenial formation in the aecium, especially numerous among macrocyclic species lacking pycnia and uredinia, and also among many microcyclic species, there is doubtless an aberration in a loosely fixed fertilizing process which is out of harmony with a morphologically stronger ontogenetic development of the species.

[1] Dikaryon (δι, two, and κάρυον, nucleus), a term proposed by Maire in 1912 (Myc. Centr. **1** : 214) for paired nuclei, for which he had previously suggested "synkaryon," which is more suitably applied among the rusts to the fusion of nuclei in the teliospore at the beginning of maturation.

Two phases in the fertilizing process. — While some investigators find the most important evidence of fertilization in the origin of the dikaryon by fusion of cells, and others in the fusion of nuclei, yet practically all include both processes as interdependent. On the one hand Blackman (1904, p. 366), who considered the cell fusions more important, stated that the fusion of paired nuclei in the basidium of the Basidiomycetes and in the teliospore of the rusts "should be considered, not as a process of fertilization, but as a purely secondary process of nuclear reduction preliminary to chromosome reduction." On the other hand Harper (1905, p. 87), who laid emphasis upon cell fusion, suggested that "the fusion-cells are perhaps morphologically vegetative offshoots of an egg-cell." Without undertaking to trace the varying opinions of different investigators it seems that a reasonable conclusion from all data at present available is "to regard the two fusions as two phases of the fertilization process in spite of their wide separation in the life history" (Sharp, 1921, p. 292).

Intermingling of hereditary strains. — The rusts are notable for great diversity of forms and habits, and for a high degree of variability within individual species. Every close student of the order soon comes to realize that no greater hereditary fixity of characters can be assumed for the rusts than for other classes of fungi, or for organisms higher in the scale of development. It has been difficult to conceive through what means a sufficient degree of variability is derived to account for the great diversity shown, while denying to the rusts bisexual or other methods of intermingling lines of parentage.

It has been customary to assert, and with apparent justification, that the life of the rusts is strongly influenced by the hosts on which they grow. The most variable and intergrading species occur as a rule upon hosts with similarly variable characteristics, *e.g.*, species of Phragmidium on roses (Arthur, 1909), Puccinia on Vernonia (Jackson, 1918c), Melampsora on Salix, etc. In the opinion of Dietel (1904), and many others, the rusts have descended from early times along with the hosts on which they are now found, and consequently have been subjected to the same environmental influences which have acted to modify the supporting hosts, and in so far have been molded into correspondingly diversified forms. In addition to the external influences the parasite has also undoubtedly responded to the changed character of the nutriment provided by the host as it underwent modification, thus establishing a direct relation between changes in the host and the parasite.

While there is a real basis of truth to be detected in the contention for

parallelism in development between host and parasite, yet the question of extended diversification and segregation into strains, which acting through long periods would create species, can be explained more fully by tracing chromosomal inheritance. In occasional forms, where nuclear fusions and reductions are lacking there can be only direct inheritance through a single line. But in most forms nuclear fusions and reductions regularly occur, and in such cases biparental inheritance would be possible, if it could be shown that the nuclei of the fusing cells were derived from independent sources (heterothallism). Demonstration of heterothallism has been effected for a number of species of the Ascomycetes, and is considered to be common in the Basidiomycetes; it has also been predicted for the Uredinales (Dodge, 1924c); Kniep, *fide* Arthur & Kern, 1926b), and in part confirmed (Craigie, 1927b, 1929). Dodge (1924c; Dodge & Gaiser, 1926) has already speculated upon some of the possibilities of heterothallic cultures, should such be found possible. The subject suggests vistas of valuable information.

Origin of heteroecism. — The phenomenon of heteroecism, or a decided change of hosts by a parasite, was well known in the animal kingdom before a name was given to it. De Bary (1865) when proposing the term called attention to the abundant occurrence of the phenomenon among cestodes and trematodes although it had not before been noted among plants. In the able treatise on heteroecismal rusts by Klebahn (1904a, pp. 1–4) many examples among the two groups of worms, as well as among pentastomes, aphids and protozoans, are cited. Mordvilko (1925, 1926) has called particular attention to the heteroecismal parallelism between rusts and aphids. Although among fungi the Uredinales exhibit the most remarkable examples of this phenomenon, yet it is known in other parasitic groups, *e.g.*, in certain Discomycetes, the best studied species being *Sclerotinia heteroica* (Woronin & Nawaschin, 1896) and *S. rhododendri* (Fischer, 1926a), and in a modified way in the Pyrenomycetes, some forms of *Claviceps purpurea* (Stäger, 1905).

In explanation of heteroecism among the rusts the views of Fischer (1898) have had much influence. He considered the ancestors of our present heteroecious rusts to have been many-spored forms and capable of living indiscriminately upon a wide range of hosts. Each species by restricting the number of hosts gradually dropped the plurivorous habit, and became confined to fewer hosts. In this restricting process the gametophytic generation sometimes became adapted to one host,

or group of hosts, and the sporophytic generation to another. If at the same time microcyclic forms were being evolved from the original autoecious progenitors, they persisted either upon the one group of hosts or upon the other.

The explanation proposed by Fischer (1898) was modified by Klebahn (1904a) and Dietel (1904) by assuming that the early forms of rusts were more or less restricted and fixed, and that the change from an autoecious to a heteroecious condition was brought about by some internal change, possibly in the nature of a mutation, which enabled the sporophytic generation to accept a very unlike host.

Orton (1927) has conceived that the highly primitive rusts originated from dimorphic algae and in passing from the free algal state to that of fungous parasites did so in such a manner that the gametophyte and sporophyte independently adapted themselves to whatever kinds of hosts were present. As parasitism became more fixed greater specialization to certain unlike species of hosts resulted. In numerous cases, however, "both the gametophyte and sporophyte selected the same host, resulting in autoecism." Microcyclic forms, it is believed, were subsequently derived by retrogression from macrocyclic ancestors.

An early hypothesis proposed by Dietel (1902), and more or less supported (Olive, 1911a; Grove, 1913a), but now largely abandoned, considered the ancestors of the rusts to have been autoecious, microcyclic, and of limited range for hosts. As they progressed in development they are conceived to have successively acquired other kinds of spores in addition to the one kind originally possessed by the species, and in doing so to have by some means established the new forms (generations) upon unrelated hosts.

Present limitations do not permit of an examination of the various ramifications of the theoretical views presented by the above and other authors. This is less to be regretted, however, as the recent admission by Fischer (1926a), following a restatement of the question, indicates that an *impasse* has been reached. He says: "in any case the problem of heteroecism in the rusts is still far removed from a definite solution." Although the method by which heteroecism originated cannot be positively formulated, yet much can be said regarding its nature.

Heteroecism a kind of specialization. — While heteroecism is a concomitant of parasitism, it is only incidentally connected with the alternation of haploid and diploid phases, as understood in mosses, ferns and higher plants. In the rusts the break in the continuity of individual existence approximately coincides with nuclear changes,

but in other fungous and most, if not all, animal parasites there is no such synchronism. If we search for some explanation of the change of hosts in worms, aphids, protozoans, and even ascomycetous fungi, the most prominent factor appears to be that of nutrition, a factor that undoubtedly lies at the basis of specialization. In fact, heteroecism can be regarded as one phase in the life of a parasite, which not only manifests itself in a marvelous discrimination in the quality of acceptible nutriment, but has gone a step farther and demands a different supply in early stages of growth from that in the later stages. This is true of all parasites showing alternation of hosts, and is quite apart from sexual phases. The refusal of the basidiospore of a rust, *e.g.*, *Puccinia graminis*, to accept the nutriment of the gramineous host which has nourished the teliospore from which it came, but will accept that of the barberry, is no more difficult to explain than (and in essence appears to be of the same nature as) the refusal of the urediniospore to accept the nutriment of another variety or strain of the same species of host from which it came. In fact, heteroecism should be regarded as only one form of specialization, a marked characteristic of parasites in both the vegetable and animal kingdoms. In the evolution of parasites some decided advantage appears to be derived by utilizing a different supply of nutriment in the early stages of individual development from that employed in the later stages. A change of food in autoecious organisms for the juvenile and adult stages is quite universal in the higher types of animals, and is clearly advantageous for the individual. Some parasites apparently get this rhythmic impulse for growth by a change of hosts, and some by a change in quality or concentration of nutriment in the same host.

PHYLOGENETIC DEVELOPMENT EARLY AND LATE

It will be well to discuss briefly the probable uredinalean phylogeny and some other related questions, in conformity with the general presentation of the nature of the rusts as given in the preceding pages. In doing so it will conduce to clearness if a distinction is made between the early or formative period antedating and leading up to the assumption of distinctively rust characters and the subsequent period during which the rusts have gradually advanced to the state of diversity and complexity now existent.

Early period in evolution. — It is self evident that in the process of evolution of any group of organisms there must be a simple

beginning. The group as it emerges from its highly primitive condition must gradually adjust itself by altered organs and modes of life, until there are evolved the distinctive features that later characterize the particular group.

In the case of the rusts, starting as independent organisms with a simple unicellular or filamentous aquatic condition, with or without chlorophyll, successive stages of greater complexity were reached until they became parasitic and gradually lost whatever chlorophyll they may have possessed. Before the beginning of this stage of parasitism the sexual process and an alternation of generations were established, together with the diversity of sporiferous multiplication in the sporophyte, which is the highly distinctive feature of the rusts. All this elaboration, this building of an inverted pyramid in development, must have taken place at such an early epoch in the world's history that no trace of it can be hoped for in geologic records.

It is to this part of rust evolution that the major part of the theorizing regarding origin is directed. The more prominent theories are briefly presented in the following paragraphs. No attempt is made, however, to follow out their modifications and transitions.

The protistan theory. — The very early period of the rusts is bound up with the developmental history of other fungi, of the algae, and of related groups. According to the views of Dangeard (1906), which are upheld by Brooks (1923) and others, the rusts together with other fungi may have been derived from simple, often one-celled organisms constituting the Protista, and consequently may have had autonomous development without the possession of chlorophyll in any stage of their history. This would constitute the fungi a monophyletic group with only a parallel relationship to the higher algae.

The algal theory. — On the other hand it is commonly assumed, following Sachs (1874), that the fungi are descended from alga-like plants possessing chlorophyll, although as an inclusive statement it is sometimes opposed (Atkinson, 1915). Vuillemin (1912) has advanced the plausible theory that the change from the algal to the fungal state began with the emergence of sea-coasts, by which some algae were abandoned to a terrestrial life. In the acquisition of the parasitic habit the need for chlorophyll was supplanted by the already elaborated nutriment readily obtained within the host. That cytologically distinct generations among both algae and fungi, and especially among the rusts should show such remarkable similarity in the vegetative forms of the two generations "probably finds its true explanation,"

according to Bower (1908, p. 81), "in the fact that the biological conditions to which they are respectively exposed are relatively uniform."

Not only is the descent of the rusts from filamentous algae, along with other fungi, indicated in the loss of a certain amount of autonomy caused by the absence of chlorophyll, but also in the mutual possession of many similar and often homologous structures and processes. Cytologic studies have supplied important data tending "to show a relationship with the Florideae" (Blackman, 1904). The aecium appears as a modified cystocarp, from which the oösphere with its sexual fertilization has vanished (Lotsy, 1907), but possessing an abundant development of conjugating cells comparable to the auxiliary cells of the cystocarp (Dodge, 1924c). The basidium is distinctly homologous with the tetraspores in the red algae, and when formed within the teliospore, *e.g.*, Coleosporium, Ochropsora, Chrysopsora, bears a close analogy to the tetraspore mother-cell (Blackman, 1904). Even that conspicuous feature of the rusts, the alternation of generations in which the alternating individuals have an independent existence, but are reciprocally derived, has its counterpart among the algae (Yamanouchi, 1906; Lewis, 1912), and in a few cases dimorphism in the two stages of the algal life-cycle can be traced (Howe, 1917, 1918).

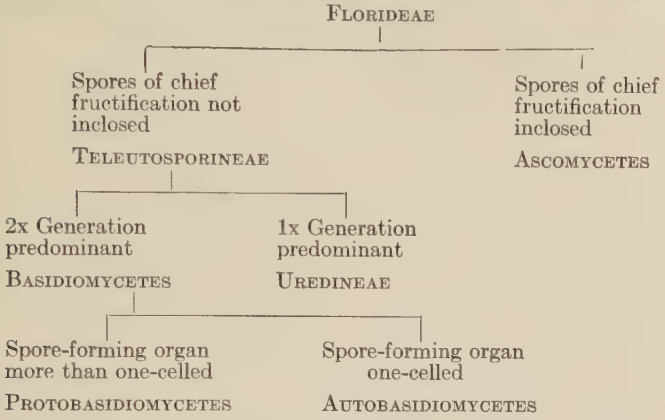
To give expression to the close relationship between algae and fungi Sachs (1874) proposed an arrangement in which the families of both the chlorophyll and non-chlorophyll series are brought together into four classes distinguished by forms of the fructification. It is supposed by the author that "in each class the fungi have diverged as ramifications from various types of algae." The rusts fall into the fourth class, thus:

IV. Carposporeae

Coleochaetae	Ascomycetes
Florideae	Aecidiomycetes
Characeae	Basidiomycetes

A more detailed outline of the phylogenetic derivation of higher fungi from the red algae has been presented by Lotsy (1907), the main features of which are shown in Table 2.

TABLE 2 — LOTSY'S DERIVATION OF THE HIGHER FUNGI FROM THE ALGAE



In explanation of this line of descent Lotsy (1907) considers that the Uredinales and Ascomycetes have a common origin and that "both have arisen from the Florideae," for the teliospore is not to be rated as a conidium, following Brefeld, "but is much more homologous to the ascus." He further considers that the dikaryon is not to be regarded as a "$2x$-nucleus, but as two $1x$-nuclei, which are united into a $2x$-nucleus just before the reduction division in the teleutospore." This makes the $1x$ condition predominant in the life-cycle of the rusts, and distinguishes them from the Basidiomycetes.

Although many writers, and among them the most recent ones (Orton, 1927), maintain the theory of the derivation of the rusts and certain other fungi from the red algae, yet there are others who think they have descended from the green algae (Janchen, 1923). The latter view has the support of some experimental data obtained by the serodiagnostic method.[1] The evolution as conceived by Mez & Ziegenspeck (1926) is shown in Fig. 45, which indicates that the several groups of the Basidiomycetes, together with the Ascomycetes and the Phycomycetes, are all derived from the green algae, and are not directly connected with the red or brown algae. Many serologic tests have shown like reactions between the higher Basidiomycetes and Vaucheria, while similar tests with the red algae (Furcellaria, Batrachospermum, Bangia) have uniformly proved negative (Neuhoff & Ziegenspeck, 1926, p. 330).

[1] This method is described in detail and illustrated with diagrams by H. Ziegenspeck. Die Bedeutung der serodiagnostischen Methode für die phylogenetisch-systematische Forschung. Bot. Archiv. **16** : 218-268. 1926.

The same conclusion has been reached by serologically comparing species belonging to the diverse genera, Peziza, Lycoperdon, Mucor and Saprolegnia, with various representatives of green, brown and red algae.[1]

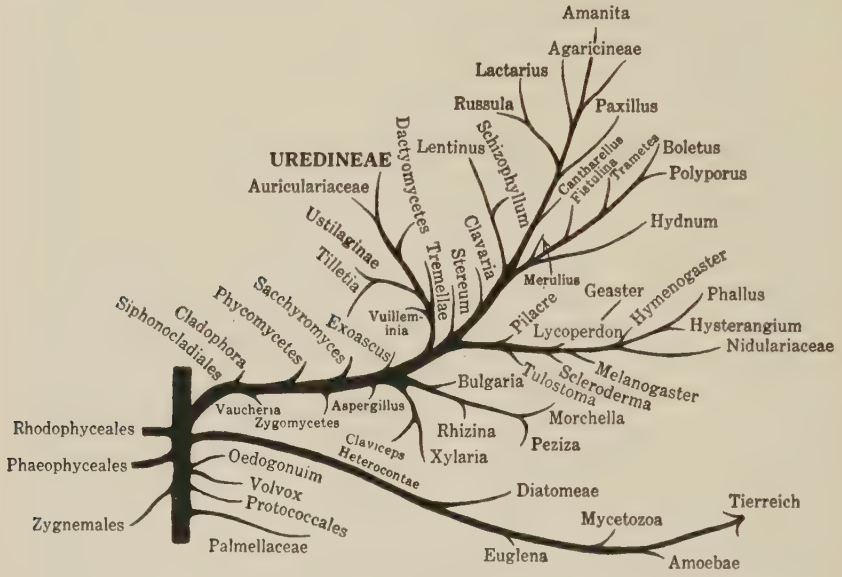


FIG. 45. — Diagram to show the evolution of the fungi through the siphonaceous green algae, and independent of the red and brown algae. (After Mez & Ziegenspeck, 1926.)

THE PHYCOMYCETOUS THEORY. — The possibility that the rusts together with the Ascomycetes have been derived from the Phycomycetes was brought forward long since by Dangeard (1895) and Brefeld (1877). This view has met with little support, not only because of the striking morphologic differences between the two groups, but because it does not afford an explanation for the persistency of the pycnia.

THE ASCOMYCETOUS THEORY. — The homologies between the rusts and the Ascomycetes were first clearly pointed out by de Bary (1884), who asserted that "the Uredineae which form aecidia belong to the series of the Ascomycetes as a special subordinate or collateral group distinguished by special peculiarities of the sporocarp" (*l.c.*, p. 308), and that their "rhythm of development" is very similar to that of the higher Ascomycetes. He based the relationship especially upon the

[1] Steinecke, F. Der Stammbaum der Algen nach serodiagnostischen Untersuchungen dargestellt. Bot. Archiv. **10** : 82–205. 1925.

general morphology of the aecium (*e.g.*, in *Puccinia graminis* and *Uromyces fabae*) in comparison with the perithecium (*e.g.*, in *Polystigma rubrum*), combined with that of the "spermogonia" in the two groups respectively. The earlier studies of de Bary led him to propose (1866b) the following grouping of the fungi, which was the first attempt to arrange their classification upon a phylogenetic basis.

I. Phycomycetes
- Saprolegnieae
- Peronosporeae
- Mucorini

II. Hypodermii
- Uredinei
- Ustilaginei

III. Basidiomycetes
- Tremellini
- Hymenomycetes
- Gasteromycetes

IV. Ascomycetes
- Tuberacei
- Pyrenomycetes
- Discomycetes

This grouping was modified in his expanded textbook of the fungi, published in 1884, as follows:

1. Phycomycetes
2. Ascomycetes
3. Uredineae
4. Basidiomycetes

The views of de Bary regarding classification were adopted by Sachs (1874), only that the rusts were called Aecidiomycetes. The idea of the derivation of the rusts from the Ascomycetes in the dominant days of de Bary and Sachs was founded upon the analogies shown by the pycnia and aecia with similar structures in the Ascomycetes.

A very much earlier suggestion of such a relationship was that of the Tulasne brothers (1847), who compared the teliospores of Phragmidium to asci. This idea was embodied in a classification by Bessey (1894), who placed the rusts among the Ascomycetes and interpreted the teliospore to be "a closely fitting ascus, containing one or more large spores" (Fig. 46), and its sorus to be "a reduced apothecium," while the aeciospores and urediniospores were subordinated as conidia.

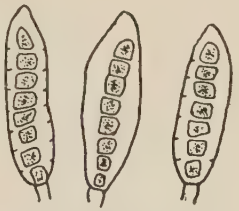


Fig. 46. — The "teleutoascus" of Bessey as represented by immature spores of *Phragmidium subcorticium*. (After Bessey, 1894.)

Cytologic studies have furnished some evidence in favor of the ascomycetous relationship of the rusts. The investigations of Christman

(1905a) and others, in establishing the origin of the binucleate condition, disclosed many similarities between the two groups. After a survey of the whole discussion regarding the origin of the rusts Maire (1911) concluded that "the primitive rust was fertilized by means of its spermatia and grouped oöspheres, and on these oöspheres was developed a very simple sporiferous structure, analogous to a very primitive ascocarp, where the spores instead of being endogenous as in the Ascomycetes, had become exogenous." Kursanov (1915, 1922, p. 120), writing somewhat later, says "one could imagine such a body as an aecidium enclosing a carpogonium (oögonium). After the fertilization of the oögonium (because of lack of information we cannot tell in what way this fertilization is effected, whether by a spermogonium, an antheridium, or by an isogamic union as in Endogone), diploid sporogenous hyphae arise, as in the Ascomycetes. The sexual function disappears in the course of further evolution, and finally the carpogonium itself disappears. The sporogenous hyphae live yet for some time," but "the majority of forms also lack the sporogenous hyphae, and each basal cell now arises in an independent manner by an apogamous fertilization." A similar conclusion was reached by Lindfors (1924) as the result of his studies.

The basidiomycetous theory. — Attention was first called to basidiomycetous characters in the rusts by Tulasne (1853, pp. 205–211), who considered the genus Gymnosporangium, then called Podisoma, "in which the different species have long been regarded as true Tremellae," to be allied to Tremella [Tremelleae] and Exidia [Auricularieae], by their method of teliosporic germination. This observation, however, was not further developed until Brefeld (1877) again called attention to the evident homology between the teliosporic promycelium and that in the Auriculariales and Tremellales, fully confirming Tulasne's observations. For some time, however, sexuality, indicated by the analogy of the pycnia and aecia with similar structures in the Ascomycetes, was held to separate the rusts from the Basidiomycetes. The latter, said Brefeld (1881, p. 170) "are, therefore, nothing else than highly differentiated non-sexual conidial forms of the Ascomycetes and Aecidiomycetes, whose asci and aecidia are wanting."

It was later (1888, p. 21) that Brefeld suggested that the character of the promycelium indicated that the Tremellineae and Aecidiomycetes might have arisen from a "common stem-form," an opinion also advocated by Van Tieghem at the same time, or even earlier, in his public lectures (Hariot, 1908, p. 5).

Brefeld at that time (1888, p. 25) separated the Basidiomycetes into the coördinate groups of Protobasidiomycetes, with septate basidia, and Autobasidiomycetes, with non-septate basidia, yet he did not include the rusts in either group. But in the following year (1889) he definitely assigned the rusts to the Basidiomycetes, as coördinate with the Auriculariaceae and Tremellineae, together comprising the Protobasidiomycetes. He now entirely rejected his former views, and considered all the higher fungi to be non-sexual. The basidium was invested with a new significance, and while in one sense a sporophore bearing conida, yet it was to be looked upon as the characteristic and fundamental organ of the Basidiomycetes. Among the rusts the pycniospores and basidiospores were to be regarded as conidia, and the spores of the aecia, uredinia and telia as chlamydospores, which possess "only a secondary and subordinate value" (*l.c.*, p. 203). In the main the views of Brefeld have prevailed as a basis for classification nearly or quite to the present time.

In 1893 Van Tieghem, confirming Tulasne's opinion regarding the basidiomycetous relationship of Gymnosporangium, arranged a classification in which the Basidiomycetes embody the basic ideas held in common with Brefeld, but with a somewhat different assortment of the families belonging to the Protobasidiomycetes and Autobasidiomycetes. The main features are given in Table 3.

TABLE 3 — VAN TIEGHEM'S CLASSIFICATION OF THE BASIDIOMYCETES

BASIDIOMYCETES
The spores arising from a basidium

Spores apical		Spores lateral	
ACROSPORAE		PLEUROSPORAE	
Basidium undivided	Basidium septate	Basidium undivided	Basidium septate
HOLOBASIDIA	PHRAGMOBASIDIA	HOLOBASIDIA	PHRAGMOBASIDIA
Lycoperdaceae Agaricaceae Tilletieae	Tremelleae	Tylostomeae	Ecchyneae Auricularieae Pucciniaceae Ustilageae

Vuillemin (1893b) further modified the same group of ideas by making the Protobasidiomycetes subordinate to the Autobasidiomycetes, in order to indicate their more primitive character.

The cytologic evidence in favor of the basidiomycetous relationship

of the rusts lies chiefly in the basidium and its nuclear behavior. Sappin-Trouffy (1896) clearly pointed out the nuclear changes in the basidium of the Uredinales, and many authors have extended the observations showing resemblance to the nuclear changes in the basidium of the Basidiomycetes. The form of the basidium and its transverse septation find such a close resemblance in the Auriculariales that the rusts are often considered to be a nearly related group and possibly an offshoot (Fitzpatrick, 1918).

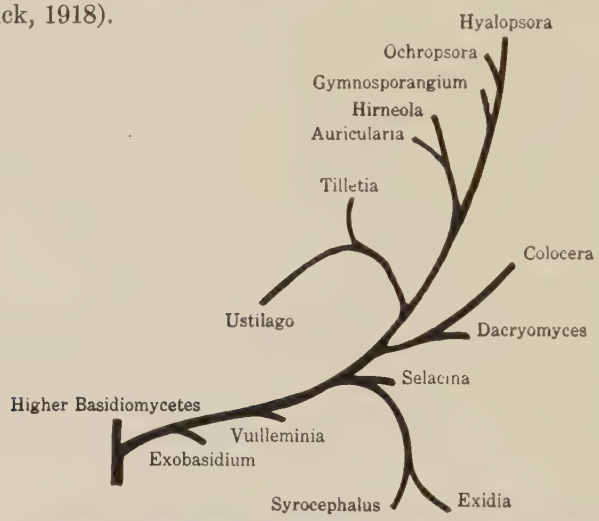
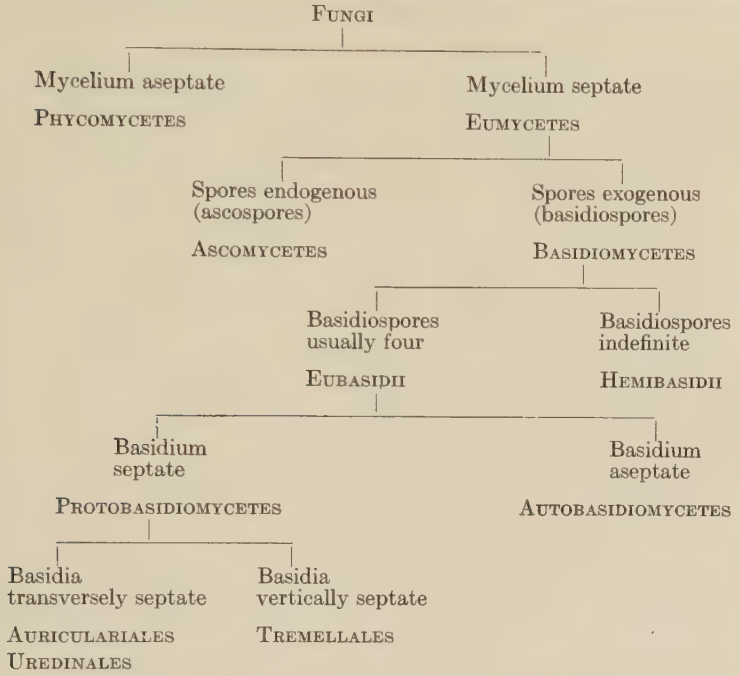


Fig. 47. — A branch of the higher Basidiomycetes, as deduced by serologic studies, showing relation of Hyalopsora, Ochropsora and Gymnosporangium to Auricularia and other presumably lower forms. (After Neuhoff & Ziegenspeck, 1926.)

Recently serologic studies have been carried out with Gymnosporangium, Ochropsora and Hyalopsora (Neuhoff & Ziegenspeck, 1926), which indicate that these genera, and presumably all the rusts, are closely allied to the Auriculariales and together with the smuts, Tremellales, Dacryomycetales and some smaller groups (Fig. 47) form one of the three or four large branches of the Basidiomycetes.

Ideas regarding the basidiomycetous relationship of the rusts have undergone many modifications at the hands of different mycologists. The predominant views at the present time regarding the phylogeny of the rusts, however, are an expansion of the fundamental opinions of Brefeld and Van Tieghem. They are embodied in the generally accepted classification adopted in Engler and Prantl's Pflanzenfamilien (Schroeter, 1897, p. 62; Lindau, 1900, p. 1), which is diagrammed in Table 4.

TABLE 4 — CLASSIFICATION OF FUNGI IN ENGLER & PRANTL'S PFLANZENFAMILIEN



SUMMARY OF THEORIES. — The theories outlined to account for the origin and early development of the rusts may be woven in the light of present knowledge into the following brief statement. Conceiving that the rusts, like the other cryptogamic groups, must have arisen in the beginning from single-celled Protista or filamentous organisms, we have the alternative of assuming that, in this formative period they either secured their energy for growth from the action of chlorophyll until becoming parasitic, or that together with other fungi they "possess some of the initial evolutionary impetus characteristic of all the primary groups of living organisms, which they hold by virtue of an early differentiation from protist organisms" (Brooks, 1923). The greater number of writers assume, however, that the power for marked evolutionary advancement was associated in all cases with photosynthesis, which requires the presence of chlorophyll. Therefore, it is generally assumed that the fungi are derived from different groups of algae, the red algae (Dodge, 1924c; Orton, 1927) usually being chosen as the progenitors of the rusts. It is sometimes further assumed,

that all saprophytes must have existed first as parasites, but that assumption, no more than its reverse statement, has little bearing upon the evolution of the rusts.

Eventually three great groups of fungi were established, Phycomycetes, Ascomycetes, Basidiomycetes, to which the Uredinales should be added as a coördinate or subordinate group. In trying to ascertain the degree of relationship of these groups and whether they arose simultaneously or in succession chief reliance is usually placed on morphologic characters, although it is necessary to bear in mind that divergence could only have occurred under primitive conditions for which present states may not afford sure indications. Owing to the wide morphologic gap that exists between the Phycomycetes and the other groups, it will do no violence to the argument to omit the Phycomycetes from present consideration. The three remaining groups show interesting features, which are contrasted in Table 5.

Table 5 — Comparable Structures in Three Groups of Fungi

Ascomycetes	Uredinales	Autobasidiomycetes
Haploid mycelium	Haploid mycelium	Haploid mycelium
Conidia	0	Oïdia
" Spermogonia "	Pycnia	?
Ascogenous cells	Fusion cells	0
Ascocarps	Aecia	0
Ascogenous hyphae	Diploid mycelium	Diploid mycelium
0	(Urediniospores)	0
Hymenium	Hymenium	Hymenium
Ascus	Basidium	Basidium
Ascospores	Basidiospores	Basidiospores
oooo oooo	oo oo	oo oo

A still closer relationship between the three groups could be shown in the table, by assuming that microcyclic rusts represent the most advanced state of uredinalean development, as undoubtedly they do. This requires a change in the table of "aecia" to "microtelia," and the omission of the line preceding the "hymenium" in all three columns. Nevertheless, the abundant diploid mycelium bearing urediniospores forms a feature of the rusts too prominent to be omitted, although unique and phylogenetically primitive.

Each of the groups possesses a haploid mycelium, from which conidia arise in two of the groups, often in abundance. In the Uredinales, however, there are no conidia in the haploid stage, unless the interpretation of Christman (1905a), Craigie (1927a) and others, regarding pycnia be accepted (pp. 120, 242), but their physiologic equivalents (urediniospores) are borne on a richly developed diploid mycelium, and have such a prominent and distinctive character as to give color and name to the whole group.

The gametes in each group, or in the rusts what may be assumed to be reduced or substitute forms of gametes, originate from the haploid mycelium, and from these are developed the main fruiting structures. The "spermogonia" (micropycnidia) in the Ascomycetes clearly correspond to the pycnia in the Uredinales, while in the Basidiomycetes there sometimes occur "on the haploid mycelium, very small oïdium-like conidia, which probably also represent old male organs" (Maire, 1911).

The ascogenous hyphae, which are present in some species of the Ascomycetes, do not appear as such in either of the other groups, although in the Uredinales some analogy can be traced between the conjugating hyphae preceding the aecium and the hyphae that result from the continued growth of the ascogenous hyphae. It is not illogical to assume that the Uredinales have lost all trace of sex organs and that consequently the formation of a dikaryophase may take place without regularity. While in macrocyclic rusts the dikaryon usually originates in the hymenium, yet in other macrocyclic species and in many microcyclic species it is largely prehymenial. From this assumption it follows that the hymenium in the rusts, and in the Ascomycetes and Autobasidiomycetes as well, is not a sex organ but a device to aid in the dissemination of spores.

Ascocarps, as they are found in many Ascomycetes, have considerable resemblance to the aecidial form of aecia, and in some respects may be considered homologous. No trace of such a structure occurs in the Autobasidiomycetes, unless it be the sporocarp.

The position of the aecial hymenium and the development which follows it constitute the most distinctive features of the Uredinales. In the higher Ascomycetes and most of the Basidiomycetes the hymenium consists of a well-defined layer of asci and basidia respectively. The asci and basidia are undoubtedly homologous, as was long since indicated by Vuillemin (1893b) and abundantly confirmed by later cytologic studies (*Cf.* Gäumann, 1928, p. 423). In the asci and basidia the process of maturation is completed by chromosomal reduction.

Usually eight or four spores are produced respectively. The spores from a single ascus or basidium are uniform in appearance, but generally diverse in physiologic properties, as proved by cultural studies with Basidiomycetes (Bensaude, 1918; Kniep, 1920; Dodge, 1920; Mounce, 1922), with Ascomycetes (Betts, 1926; Shear & Dodge, 1927; Wilcox, 1928), and finally with Uredinales using *Puccinia helianthi* and *P. graminis* (Craigie, 1927b). The four basidiospores and eight ascospores may be divided into two groups, or sexes, of two or four spores each respectively. There are also indications that each spore from an ascus or basidium possesses physiologic properties differing from each of its neighbors, which has led to the assumption that such fungi have "four sexes," or possibly twice that number in Ascomycetes. Furthermore, the chromosomal relations and hereditary nature of the spores of a single basidium or of a single ascus may eventually be found to be more complex than present investigations have revealed.

The product of the aecial hymenium in the Uredinales is at first not an ascus or basidium, but a binucleate spore. In the macrocyclic species this spore may originate a mycelium of binucleate cells with urediniospores capable of repeating the process. In microcyclic species no mycelium is formed, but only a spore, which like the teliospore of the macrocyclic species, produces a basidium. The basidium of the rusts is in its essentials the homolog of the ascus of the Ascomycetes and the basidium of the Basidiomycetes (Kniep, 1911). It gives rise to four basidiospores, presumably separable into two physiologically diverse groups of two each, although such a distinction still awaits full demonstration.

Bearing in mind these features as they occur in the three groups of fungi, it is not difficult to make fairly plausible assumptions regarding the origin of these groups in point of time.

(1) By giving prominence to the elaboration of sexual features in the first column, and their successive disappearance in the other columns, the theory of the earlier origin of the Ascomycetes, and then the successive development of the other two groups, finds abundant support.

(2) If attention is given to the highly organized character of the Uredinales, and especially to the unparalleled diversity of forms in the diploid stage, the Uredinales are a more recent evolutionary development, arising either from or near the Ascomycetes, indicated by the pycnia, or less likely from the Basidiomycetes, indicated by the basidia.

(3) If the basidium with its maturation process is thought to be most important, then the rusts are to be grouped with the Basidiomycetes, and not far from the Auriculariales. Although there are many reasons to believe "that the Hymenomycetes phylogenetically are a rather young group" (Kniep, 1917), yet it is probably most satisfying to say with Maire (1911) that "the Basidiomycetes and the Uredinales have a common origin, which should occur on the same level with the ancestors of the Ascomycetes."

(4) If, however, assuming that the three groups of fungi have arisen from the algae, either the red or the green, it seems probable that the group retaining in its morphology more of the characteristically algal features should be considered the oldest, and to have been the earliest offshoot from the main stem. Such a morphologic test places the Ascomycetes as the first branch, followed by the Uredinales and then the Autobasidiomycetes. The last group, having in comparison a later origin, has developed, like the Compositae among flowering plants, into a vast number of diverse forms, while the rusts, with a somewhat more ancient lineage than the Autobasidiomycetes, and restricted by parasitism, have greatly elaborated the sporophytic stage, but following the evolutionary direction indicated by the other two groups, lean toward its reduction.

The varied theories regarding the evolution of the rusts have recently been presented and discussed from a number of different angles (Gäumann, 1928) with a fullness and clarity not feasible in the present connection.

Without pursuing further the question of the origin and early phylogeny of the rusts, we may turn to their later evolution.

Late period in evolution. — The period of modern development, as here understood, begins with the advent of so-called "primitive rusts," that is, the time when the phylum was sufficiently differentiated to show the main characteristic features, and extends up to the present day. It has embraced a not inconsiderable portion of geologic time. The very meager record so far gleaned from the rocks, however, is too uncertain to be of value (p. 204).

Progressive development. — The two outstanding features of the late period have been a progressive and diversified evolution in some characteristics combined with a strong retrogression in others. Both forces are still in active operation. No existing species can be considered truly primitive, that is, having wholly or in large part the characteristics of rusts that flourished in early geologic times. Our

idea of such forms must be derived from species that still live upon hosts which were dominant in the early period, and which presumably retain more primitive characters than rusts now growing on hosts of later origin. In this manner we select the fern rusts (Dietel, 1904) from which to start in our study of evolution, and especially the genus Uredinopsis. Unfortunately both the morphology and physiology of the group of rusts to which Uredinopsis belongs, the Pucciniastreae, have only begun to receive adequate attention. We are able to gather, however, that the early rusts had the several sorts of sori and essentially the same succession of spore-forms as those in groups of later development, and, moreover, were heteroecious. The aecia were especially prominent, possessing a highly developed protective envelope.

Progressive differentiation is shown in the complexity of the telial sori and in the endless forms and ornamentation of the spores.

Comparing the fern rusts with the heteroecious grass rusts, the latter taken as representative of a later origin, and the two standing for the great divisions of Melampsoraceae and Pucciniaceae, it is possible to predicate a simpler development for the former, and more marks of complexity for the latter. In a very general way the Melampsoraceae exhibit telia that are more or less compacted, the teliospores vertically septate or more usually without septa, lacking a pedicel, or when in chains without disjunctive cells. The teliospores as a whole are not deeply colored or indurated, and are without sculpturing. Contrasting the Pucciniaceae, the latter show the telia more often well exposed and loose, and with the teliospores usually pedicelled, and transversely septate. The teliospores as a whole are much indurated, deeply colored, and the sculpturing firm and prominent.

What is here said to contrast the two great groups of the rusts, will also apply with almost equal force to the sub-families and to the genera that represent the highest and lowest development in each group. It should also be said that the rusts in general have shown, beside the morphologic changes in sori and spores, a progressive increase in physiologic specialization.

Retrogressive development. — Superposed upon the progressive development previously indicated, and especially evident among members of the Pucciniaceae, has been a retrogressive evolution, shown in the dropping out of spore-forms, shortening of the cycle, and in the loss of a sharp distinction between gametophytic and sporophytic alternation. This change has simplified the cycle of development through decline of the sporophyte.

From many lines of evidence we feel justified in assuming that the rusts reached the peak of their evolution many epochs ago, not long after the time when they had become strictly endoparasitic. They doubtless uniformly possessed at that time a variety of spore-forms and a less restricted choice of hosts than at the present time. Beside a change in the cycle, a simplification of structure has taken place as shown in the decline or omission of the protective envelope of both aecia and uredinia.

Effect of parasitism. — Parasitism as a mode of life has had a marked bearing upon the development of the rusts in essentially the same manner as it has acted upon other internal parasites, both animal and plant. The abundance and uniformity of the food supply and the protected environment supplied by the tissues of the host have reduced the need and consequently the competitive selection leading to variation in the form of the vegetative body. At the same time the fixity of habitat and restriction of the organism to a few species of hosts, these hosts also to a somewhat less degree having a fixed habitat, has emphasized the need and competitive possibility for diversity and facility in reproductive and distributive processes. The rusts, like animal parasites and most saprophytes, show a degradation or simplification of the vegetative structure, but at the same time a marvelous amplification of the reproductive system. The mode of life has disturbed and exaggerated the balance between vegetative and reproductive activities greatly in favor of the latter as compared with non-parasitic plants. At the same time there has taken place in the microcyclic group of species a pronounced decline of the sporophyte. This is roughly the converse of what has taken place in independent plants, where it is the gametophyte that has retrogressed. The rusts abundantly bear out the statement that parasites "may be regarded as in a sense extremely high in organization."[1]

Omission of spore-stages. — There are species, *e.g.*, the west-American *Uromyces suksdorfii* on Silene, which produce all spore-forms in early spring, but as the season advances urediniospores cease to appear. Still later even the aeciospores become partly or even wholly suppressed, and only teliospores are formed. The same series of changes may be associated with latitude or altitude, *e.g.*, the European *U. acetosae* usually shows all spore-forms southward, but only teliospores far northward or on summits of high mountains. Such varia-

[1] Caullery, M. Parasitism and symbiosis. Ann. Rep. Smiths. Inst. (1920) p. 405. 1922.

tion in spore production may be ascribed in large part to changes in the conditions for growth of the rust (pp. 242–246).

A seemingly anomalous situation may be brought about, by which the gametophytic mycelium, after producing teliospores associated with aecia for a time (Fig. 48), will later form only teliospores from the same mycelium. It is probable that in all, or nearly all, such instances the teliospores arising from the uninucleate mycelium (Fig. 49) are to be rated as macrocyclic, although simulating in mode and form of production a microcyclic rust. This has been found to be true for *Puccinia podophylli*, providing the only recorded test of this assumption that has yet been made. *Puccinia podophylli* is a macrocyclic species without uredinia. The aecia and telia alternate to form two generations. Sometimes, however, telia are associated with the aecia upon the same uninucleate mycelium, and sometimes, when the infection is on thin basal leaf-sheaths or other early maturing parts only teliospores are produced. Cultures of the teliospores, whether borne on the binucleate or uninucleate mycelium, give rise to aecia when favorably grown (Whetzel, Jackson & Mains, 1925), indicating that there has been no genetic change in the character of the teliospores, all being of a macrocyclic nature, however derived.

Fig. 48. — Section of a grass leaf with teliospores of *Puccinia graminella* arising from the sides of an aecium. (After Dietel, 1897a.)

The suppression of uredinia has become a fixed condition in many species of Puccinia, such as are included in the genus Allodus of the Arthurian system, and in practically all species of the large genus Gymnosporangium, as well as in many species of other genera. If

the suppression of both aecia and uredinia should become a fixed condition, that is, if only one kind of spore were produced by the gametophyte, which again in the succeeding generation gave only one and the same kind of spore, the conversion of a macrocyclic into a microcyclic species would be accomplished. No such transformation has yet been proved to occur, although logically possible, and in the blackberry rust, *Gymnoconia interstitialis*, the appearance of such a change has been noted (Dodge, 1923a).

FIG. 49. — Teliospores arising from uninucleate mycelium beside an aecium of *Uromyces acetosae*. (After Lindfors, 1924.)

SHORTENING OF THE LIFE-CYCLE. — Doubtless the most conspicuous evidence of degeneracy among the rusts is the curtailment of normal spore-production, having its seat in the shortening of the life-cycle by the elimination of the mycelium in the sporophyte. A microcyclic condition results when no mycelium is formed in the sporophytic stage and only one form of spore becomes possible, other than the pycniospore. Circumstantial evidence that microcyclic species have been derived from macrocyclic species is found in the presence of a few aeciospores or peridial cells in the microtelia of certain species, *e.g.*, *Uromyces scutellatus* and *Puccinia grindeliae*. The readiness with which aecia and uredinia are suppressed by external conditions in many macrocyclic species (p. 245), and the fact that many species appear to have lost the power to form uredinia, give a logical basis for the assumption that there is a general tendency among the rusts to become microcyclic. It is easy to believe that such a change is actually taking place in certain instances at the present time, although actual proof is not yet established.

Correlation. — The changes which appear to be taking place at the present time in shortening the life-cycle of certain rusts, or in reducing the number of cells in the teliospore, have undoubtedly been in operation for a long time, and have doubtless brought about firmly established races or even forms that are now rated as species. It may be assumed with much plausibility that all species of Uromyces have been derived from similar species of Puccinia, and that all microcyclic species have descended from similar macrocyclic species. In some instances the original form may have become extinct, as appears to be true of nearly all species of Uromyces on leguminous hosts. In other instances considerable divergence has resulted, so that the Uromyces or the microcyclic rust does not exactly agree morphologically with the present form representing the original from which they were derived. Species that correspond as indicated are said to be correlated (Orton, 1912; Travelbee, 1915).

The close morphologic resemblance between certain microcyclic species and the telia of certain macrocyclic species has been recognized for a long time. Dietel (1897a) remarked the similarity of teliospores of *Puccinia mesneriana* on Rhamnus and *P. coronata* on grasses, the latter having aecia on Rhamnus, and also the same correspondence between *P. ornata* on Rumex and *P. phragmitis* on grasses, with aecia on Rumex. Like observations were independently made by Fischer (1898), and a list of thirteen pairs of species, partly illustrated with figures, in addition to those mentioned by Dietel, were made the basis of a discussion of their phylogenetic derivation, in which the species with uredinoid aecia of the type of *P. hieracii* were included. Such correlation was later made the means (Tranzschel, 1904) for predicting similar relationship in still other species (p. 55). In one instance a chemical reaction has been found (Mains, 1922a) to supplement the morphologic and host indications of relationship. The pedicels of the spores in *Puccinia moreniana*, a microcyclic form on the West American liliaceous host Brodiaea, stain blue upon the application of iodine, and a like reaction takes place in the macrocyclic *P. pattersoniana* on Agropyron and other grasses, with aecia on Brodiaea (Fig. 50).

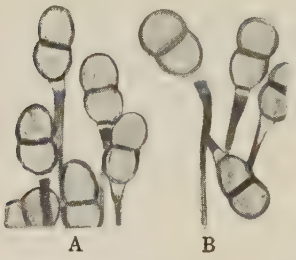


Fig. 50. — Pedicels stained with iodine, except next the spore: *A* teliospores of *Puccinia pattersoniana; B* microteliospores of the correlated *P. moreniana*. (After Mains, 1922a.)

When the correlation is between autoecious species of Uromyces and Puccinia with intergrading forms, *e.g.*, *U. pulcherrimus* and *P. heterospora* (Fig. 51), occurring on Malvaceae, it is customary to include both forms under one name. But similar heteroecious species are listed separately, *e.g.*, *U. peckianus* and *P. subnitens*, both with uredinia and telia on the grass Distichlis and aecia on various Chenopodiaceae and other hosts (Fig. 52). It is sometimes possible to correlate microcyclic species differing from one another in hosts and to some extent in morphologic characters with the races of a macrocyclic species, *e.g.*, *Puccinia seymeriae*, *P. pentstemonis* and *P. comandrae* and three races of *Puccinia andropogonis*. In many, or one might say, most instances, however, the short-cycle rust cannot at the present time be correlated with its probable long-cycle form, and therefore must necessarily be maintained as a separate species, whatever views may be held regarding the advisability of uniting correlated species under one name.

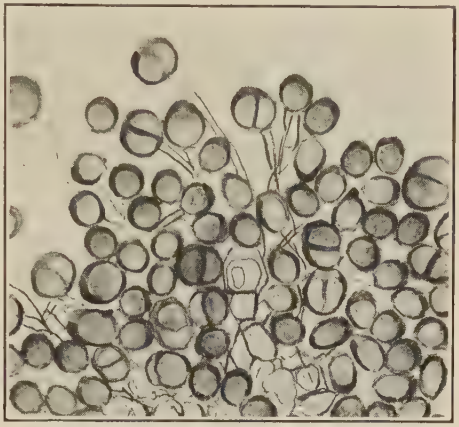


FIG. 51. — *Puccinia heterospora*, with one- and two-celled spores in the same sorus, the former predominating. Pedicels often attached obliquely. (After Holway, N. Am. Ured. pl. 27.)

CLASSIFICATION

"The organisms of the present represent a cross-section of the lines of descent. . . . The modern classification of animals and plants is an attempt to arrange the groups of individuals in a system which shall represent their genetic relationships."[1] For this purpose relationship is usually interpreted in terms of morphology. Yet it must be borne in mind that resemblances in structure are by no means a sure criterion of relationship, as Lotsy (1916) well illustrates by calling attention to the common observation that "sisters can be more dissimilar than two girls of quite different extraction." This fact is found to be especially true among the Uredinales where a strict adherence to morphologic

[1] Hitchcock, A. S. Methods of descriptive systematic botany. 216 pp. 1925.

characters sometimes leads to wide separation of forms undoubtedly possessing close relationship. We can accept the statement of Vuillemin (1907) when beginning a discussion of the true basis for classification in mycology, that "the classification of fungi is based upon the same principles as the classification of other living things. It encounters the same initial difficulty: the whole manifestation of life consists of changes,

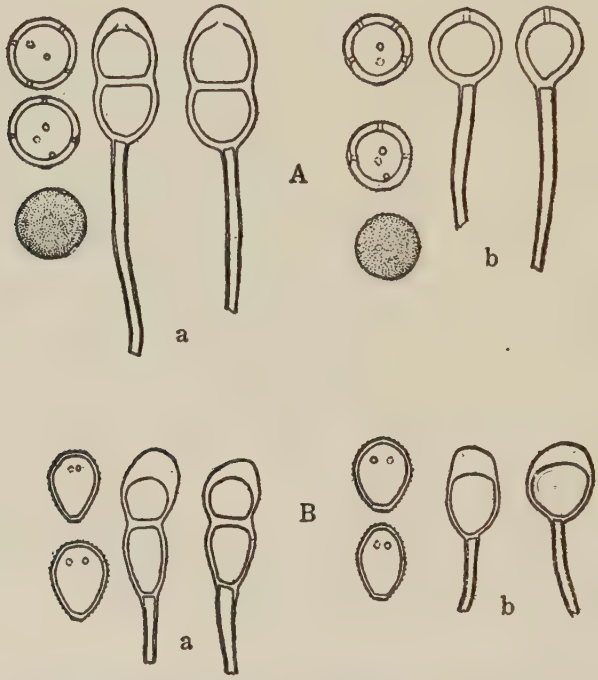


Fig. 52. — Correlation between species of Puccinia and Uromyces: urediniospores and teliospores *Aa* of *P. subnitens* and *Ab* of *U. peckianus*, both on Distichlis; same *Ba* of *P. asteratum* and *Bb* of *U. perigynius*, both on Carex. (After Orton, 1912.)

movements, displacements, while the whole system [devised for classification] searches for points of fixed comparison." Brierley (1919, p. 215) expresses the difficulty confronting the systematist in these words: "the species is a dynamic relation and not a static figure; it is an event and not a thing."

Among the rusts the need of recognizing variables and an unstable polymorphism probably enters into the species concept to an extent scarcely paralleled in other groups of fungi and almost inconceivable in higher plants.

PERFECT CLASSIFICATION IMPRACTICAL. — The ideal classification would take into account all characters, both morphologic and physiologic, including the degree of fluctuation shown by successive generations. But intimate knowledge of the forms to be classified is always too limited, even if so comprehensive a method were practical, to enable such a course to be successfully pursued.

SPECIES THE UNIT OF CLASSIFICATION. — In all classifications the species is made the unit from which all larger and lesser groups are constructed. It is generally recognized, however, that there is no fixed criterion by which a species can be defined. It ought to embrace individuals of identical constitution and form, but probably under close scrutiny such groups could not be found in nature, or if they occur would not be recognized. As classification is not only for the purpose of showing affinity, but as a convenience in identification, the making of species and their several groupings in practice rests largely upon morphologic characters with a minimum influence from the physiologic side. A definition by Wettstein (1901–08, p. 13) corresponds well to the philosophy usually accepted by the systematist. He says: "one is able, therefore, to designate as species the totality of individuals which agree among themselves and with their offspring in all characters that appear to the observer to be essential." But how is the observer to recognize "essential" characters, unless we assume that he has a special instinct in this direction? The difficulty is not materially reduced if we accept the definition for a species ("linneon," he calls it) given by Lotsy (1916), as "the total of individuals which resemble one another more than they do any other individuals." Another definition of a species as "a group of individuals of common descent with certain constant characters in common which are represented in the nucleus of each cell by constant and characteristic sets of chromosomes" (Hurst, 1927), will probably never be of service in uredinology because of the small size of the chromosomes which makes the study of their characteristic complexes difficult.

None of these definitions meets practical requirements for distinguishing species among the Uredinales, since the problem here involves combining into genera, species, etc., not only the diversity and intergradation of morphologic forms, in many cases reminding one of the perplexities met in Rosa, Rubus, Viola, Crataegus, and other phanerogamic groups, but in addition satisfying the physiologic requirements of strict parasitism embracing a delicate specialization and heteroecism with its unrelated hosts, for which the phanerogamic botanist has

little or no counterpart. Furthermore, account must be taken of the length of the life-cycle and the degree of simplification, which may vary in the same genus or species even to the near extinction of the sporophyte, entailing a limitation in the number and character of the spore-forms. The morphology, the specialization and the degree of retrogressive development enter into the conception of every species of rust, not only as static factors but in a mutable and kaleidoscopic diversity.

Influence of host in determining species. — There is still another serious difficulty in addition to that of variation and pleomorphy in deciding the boundaries of species among the rusts. It is clearly impractical to assort the rusts entirely apart from their hosts. In fact, it was pointed out by de Bary (1863a) that the rusts exercise a most rigorous choice in the selection of hosts, and that, for example, the differences between the aecial forms of *Chrysomyxa ledi* and *C. rhododendri* so far as he could detect them were so slight that they were "more biologic than morphologic species." Not long afterward Schroeter (1879, p. 69) called attention to similar conditions in *Puccinia caricis*, which he said were likely to shake current views regarding species as held by many mycologists of the time.

The expression "biologic species" was used for forms morphologically similar but physiologically distinct by Klebahn in 1892 and Rostrup in 1894. In 1893 Schroeter proposed "sister species" (*species sorores*), the next year Hitchcock and Carleton (1894, p. 4) suggested "physiological species," Eriksson (1894) "specialized forms" (*formae speciales*), and Magnus (1894) "adapted races" (*Gewohnheitsrassen*). In 1896 Rostrup changed his earlier term to "biologic races" (*biologiske Racer*). The expression "physiologic races" is adopted in the present work (p. 252), and is interpreted to apply to forms that are morphologically almost or quite indistinguishable, but with hosts that although closely related for one or the other antithetic stages are not interchangeable. Such forms, largely detected by experimental cultures, were for a time, and still sometimes are, described and named as species. No generally acceptable practice has been reached in such cases, but there appears to be a tendency to employ varietal or racial names in form of a trinomial, following to some extent the method introduced by Eriksson (1894), *e.g.*, *Puccinia graminis tritici*, etc., and further to separate the races into "physiologic forms" (p. 255). For the latter term Scheibe (1928) proposes "biotype," as more concise. Such secondary forms are often of much economic importance. They are usually designated

by numbers or letters, more rarely by Latin names. Beside the various aspects of the subject of physiologic races or forms as influencing classification (Arthur, 1908b; Mains & Jackson, 1926), there are still other problems involved of equal importance.

Influence of correlation on species and genera. — It appears to be a logical conclusion that forms having the same ancestry should be assigned to the same species. If the relationship of correlated species (p. 100) is recognized, the necessity is involved of placing such species under a single name, which also requires in most instances a change in genera, *e.g.*, the name *Uromyces peckianus* would drop into synonymy and the form be listed as a subspecies, or the one-celled teliosporic race, of *Puccinia subnitens*. The generic names Micropuccinia, Calliospora, Ameris, Necium, Cionothrix, and many others maintained for microcyclic species exclusively, would probably be abandoned. Such a method is already in practice with many uredinologists when dealing with the matter of generic names founded on life-cycles, but is rarely utilized for species founded either on life-cycles or on teliosporic variation. Such a reform will be necessary before a rational classification can be established.

Species according to early methods. — It was a comparatively easy matter to make descriptions of species in the days when each spore-form was thought to represent a distinct species. The method was pursued long after de Bary (1863a) showed that many rusts have a polymorphic existence, and forms that had appeared to belong under two or three genera might be stages in the life-cycle of a single species. In the minds of some mycologists the convenience of designating each spore-form by a separate genus and species name (Saccardo, 1904), even when the other forms in the life-cycle are known to the author, quite outweighs other considerations and has been continued in practice to some extent up to the present time. It is now almost universally accepted that the complete description of a species should include all of its spore-forms, although in practice this is not always feasible.

Exaltation of the pycnia. — For a short period the pycnia were made the primary basis of classification, although later dropping out of use. De Bary in his earliest work (1853) proposed the following scheme, in which only one kind of sorus in addition to pycnia was recognized as constituting a species. The genus Gloeosporium is not a member of the Uredinales.

Aecidiacei, accompanied by spermogonia.
Aecidium, Roestelia, Uredo suaveolens, Uredo orchidis, Physoderma (Uredo) gyrosum.

Uredinei, unaccompanied by spermogonia, spores readily detached.
Monospori: Spores single.
Trichobasis, Epitea.
Seirospori: Spores catenulate.
Gloeosporium, Podocystis.

Phragmidiacei, unaccompanied by spermogonia, spores not readily detached.
Uromyces, Puccinia, Phragmidium.

Dimorphism made prominent. — In the middle of the last century Tulasne (1854a) brought forward much experimental and observational data to show that the teliospores and urediniospores were not independent organisms, neither was the one parasitic upon the other, as then generally considered, but that the two forms constituted two phases of one species. He therefore concluded that the rusts were dimorphic. The following classification proposed by Tulasne (1854b), which has been a basis for all subsequent schemes, did not recognize the pycnia as important, but gave chief place to dimorphism. Cystopus was doubtfully included and later excluded.

Uredinei

1. Albuginei, spores of various forms, white or whitish.
   1. *Cystopus* Lév.
2. Aecidinei, spores of one form, with peridium.
   2. *Caeoma* Tul.; 3. *Aecidium* Lk.; 4. *Roestelia* Reb.; 5. *Peridermium* Lk.
3. Melampsorei, spores of two forms, compact, cushion-shaped.
   6. *Melampsora* Cast.; 7. *Coleosporium* Lév.
4. Phragmidiacei, spores of two forms, pulverulent, dark, usually in circles.
   8. *Phragmidium* Lk.; 9. *Triphragmium* Lk.; 10. *Puccinia* Lk.; 11. *Uromyces* Lk.; 12. *Pileolaria* Cast.
5. Puccinei, fruits of one form, naked, fleshy, ligulate, or tremelli-like, usually large.
   13. *Podisoma* Lk.; 14. *Gymnosporangium* DC.
6. Cronartei, spores of two forms, with peridium, ligulate, generally preceding the chief form.
   15. *Cronartium* Fr.

In the interpretation of the groups Tulasne followed Link (p. 45), but rejected Link's expansive treatment of "Caeoma," and made the name apply only to aecial forms. In selecting names for his families the fifth family reflects the views of Micheli, but the genus Puccinia

retains the character accorded it by Persoon and not that of Micheli, and consequently does not fall into the family Puccinei.

Supremacy of the teliospore. — After the rusts were placed among the *Basidiomycetes* by Brefeld (1889) and this assignment endorsed by Van Tieghem (1893), the teliospore was accepted as the most significant of all the spores and nearly all subsequent classifications have been based upon it. So firmly has this understanding of its significance become fixed in the minds of mycologists and other botanists, that in the International Botanical Congress at Brussels in 1910 a majority vote established the questionable rule[1] that "generic and specific names given to other states [than the teleutosporic] have only a temporary value." The pycnia, aecia and uredinia thus become relatively unimportant, both in the grouping of genera and the description of species, even their presence or absence often being deemed systematically inconsequential.

Vuillemin (1893b) constituted the basidium with its spores a palingenetic character with primary significance. In accordance with this idea a revised classification by Van Tieghem (1898) divided the rusts into two families: (1) Coleosporieae, to include genera having the basidium internal, and (2) Puccinieae, having the basidium external.

Various modifications of these several ideas were embodied in classifications by different authors, but the arrangement by Dietel (1897a, 1900) in Engler & Prantl's Pflanzenfamilien, has been generally accepted as the basis of subsequent studies. Dietel supplied the name Uredinales for the order (1897a, p. 24). In his improved classification (1900, p. 547) he placed the rusts in four families, as follows:

A. Melampsoraceae, teleutospores sessile, single in the tissues or united into a crust.
Uredinopsis, Pucciniastrum, Melampsoridium.

B. Coleosporiaceae, teleutospores sessile or with a broad hypha-like stalk, in waxy crusts of one or two layers.
Ochropsora, Mikronegeria, Coleosporium, Stichopsora, Chrysopsora.

C. Cronartiaceae, teleutospores sessile, catenulate.
Phakopsora, Schroeteriaster, Barclayella, Chrysomyxa, Trichopsora, Cronartium, Alveolaria, Masseeella, Dietelia, Endophyllum, Pucciniosira, Didymopsora, Coleopuccinia, Pucciniostele.

D. Pucciniaceae, teleutospores pedicelled.
Gymnosporangium, Hemileia, Uromyces, Puccinia, Gymnoconia, Diorchidium, Sphenospora, Phragmopyxis, Phragmidium, Triphragmium, Sphaerophragmium, Anthomyces, Ravenelia.

[1] Briquet, J. Régles internationales de la nomenclature botanique. 1912. *Cf.* pp. 28, 47, 69.

In a still later arrangement Dietel (1928) has reduced the number of families to two, Melampsoraceae and Pucciniaceae, with 19 genera distributed in five tribes for the first family, and 83 genera in fifteen tribes for the second family.

The Uredinales were divided by Grove (1913b) into the *Impedicellatae*, with teliospores sessile: Melampsoraceae, Cronartiaceae, Coleosporiaceae, Endophyllaceae; and the *Pedicellatae*, with teliospores pedicelled: Pucciniaceae.

Introduction of biologic characters. — Biologic characters were brought forward by Schroeter (1870, 1889) by means of which each genus could be divided into sections in accordance with the number of spore-forms in the species included (p. 56).

A classification by Arthur (1906a, 1907–27) combined morphologic and biologic characters, and was based upon the recognition of the full life-cycle of every species. It was assumed that in the evolution of the rusts a definite and stable state of development had been reached that would justify the segregation of genera on the basis of the length of the life-cycle. Consequently the genera in each tribe were grouped as:

(1) Eugyrineae, with pycnia, aecia, uredinia and telia.
(2) Aeciogyrineae, with pycnia, aecia and telia.
(3) Urogyrineae, with pycnia, uredinia and telia.
(4) Teliogyrineae, with pycnia and telia.

It was recognized that sometimes the pycnia might not be produced, but that the other spore-forms of the respective groups would likely be present. In order logically to carry out this plan it was necessary to introduce more generic names than ordinarily recognized, so that each genus should possess only one kind of life-cycle.

The assumption that the length of life-cycle has become a fixed state in the evolution of rusts has been shown by subsequent studies not to be well founded. The presence of any spore-form other than the teliospore or microteliospore is now considered to be more or less an adaptation to internal or external conditions (Fischer, 1907; Morgenthaler, 1910). Nevertheless, the distinctions advocated by Schroeter and Arthur have had an important part in stimulating experiment and observation relating to the full developmental history of individual species. Recently the method pursued by Arthur has been in part endorsed and somewhat extended by Sydow (1921, 1922).

Reviving interest in the systematic importance of the pycnia and aecia, and placing them in reciprocal relation with the telia, together with

emphasis placed on a combination of characters rather than unduly emphasizing the teliospore, were factors of value in the Arthur classification.

TIME NOT RIPE FOR A NATURAL CLASSIFICATION. — It is the general opinion among the best informed uredinologists that there is not yet enough information regarding the intimate life history of a sufficiently wide range of types of rusts and adequate unanimity regarding the theoretical course of their ontogenetic and phylogenetic development to make it possible to formulate an acceptable classification showing natural affinities and having practical diagnostic features. The true basis for such a classification was recognized long ago. In the French translation of the third edition of Sach's *Textbook of Botany* (1873) Van Tieghem makes the important comment that the characterization of any family of fungi should be based upon (1) the mycelium or vegetative part, (2) the sexual and asexual reproductive structures, and (3) the order of appearance of the forms of fructification as determining the succession of generations. Such a course would lay a solid foundation for a natural classification of the rusts.

In the light of present knowledge these requirements may be annotated as follows: (1) It is not yet known how much diversity exists in the rust mycelium, but such characters as may be derived from it should not be ignored. (2) The essential morphologic unity of aecia, uredinia and telia is to be recognized, and that aecia and telia are of equal ontogenetic significance. (3) The stability in differentiation of organs, *i.e.*, sori and spores, far exceeds the stability in sexual expression. (4) Microcyclic species are derivative of existing or extinct corresponding macrocyclic species.

A species is a variable quantity, composed of groups of individuals, races and varieties of greater or less morphologic and physiologic resemblance. A species name applied to any part or state of a fungus automatically becomes the name of the species in its entirety. A recent statement (Arthur, 1929) sets forth the following six prerequisites to be borne in mind for securing an approximation to a phylogenetic arrangement of the rusts: (1) Clear understanding of specific individuality; (2) Recognition of diversity of forms within the species; (3) Correct interpretation of homologies; (4) Evaluation of characters; (5) Extent of retrograde development; and (6) Theory regarding ancestry.

NOMENCLATURE

It is self-evident that the study or discussion of any topic in natural history involves the employment of names to designate the objects involved. To be of general service the names must have an unvarying application. Such a requirement is generally recognized, and its expression was formulated more than a century ago by an eminent botanist of wide and varied experience, who said: "In order that a nomenclature become universal, it must be fixed, and the fixity of that of natural history is founded on the . . . principle . . . that the first one who discovers an object, or who records it in the catalog of science, has the right to give it a name, and that this name must be necessarily accepted, unless it already belongs to another object or transgresses the essential rules of nomenclature" (DeCandolle, 1813). This statement recognizes what is now called the "law of priority," and embodies a principle that has been tacitly or actively upheld by all organized bodies of botanists and most individuals who have given attention to the subject. Although such a method of establishing the correct name of a plant would seem a simple and reasonable procedure, yet in practice it is often ignored and has been found difficult and unacceptable in many instances, in large part due to lack of a generally approved code of "the essential rules of nomenclature."

It must be conceded that the most important "rule" should be one indicating the "object" to which the original name was applied. Until within a comparatively few years a species or genus was considered to be a stated concept reflecting the characteristics of certain organisms in nature. As the concept changed with different individuals the application of the name necessarily shifted. This is well illustrated by the history of the genus Puccinia. The name proposed by Micheli (1729, p. 112) applied to a conical gelatinous outgrowth containing pedicelled spores. Two examples were cited and figured, the more prominent one being the species now called *Gymnosporangium clavariaeforme*, growing upon the branches of Juniperus. Persoon in 1794 (*l.c.*, p. 119) adopted Micheli's conception of the genus in part, but gave more attention to the spores than to the matrix in which they occur. He added many examples, the most prominent being that of *Puccinia graminis*, as now understood. Eleven years afterward the genus Gymnosporangium was erected to include two-celled spores in a gelatinous matrix, and one of the species included was the one on which Micheli had established the genus Puccinia. Thus it came about that the object and its allies to which the name Puccinia was correctly applied for over

three quarters of a century no longer bore the name, due to shifting concepts; and the misapplication has continued to the present day.

In order to avoid the shifting of names to correspond with the shifting of concepts and to bring about a reasonable fixity in their application a group of botanists some three decades ago proposed that the name of a species should invariably go with the specimen used in describing the species, and the name of a genus should apply specifically to the species on which it was founded, that is, the use of "types," a method of stabilizing names that in principle has met with general favor.

A difficulty in the application of the method arises when the author has included more than one form under a specific name and has failed to preserve a specimen or designate the particular form chiefly intended, or has similarly placed more than one species under a genus. Rules have been formulated to meet these difficulties, but up to the present time have not met with general approval. A further difficulty has arisen in the application of the law of priority in that it sometimes displaces well known and universally recognized names by obscure names that are found to have had an earlier publication, or by familiar names of different application.

Another difficulty is sometimes encountered, especially in dealing with pleomorphic fungi, from the failure to recognize that the name applied to a part or stage of a plant becomes automatically the name of the whole and every part of the plant, whatever the form may be. Among the rusts the debarment of names not originally applied to the teliosporic form (p. 107), therefore, is heterodox, and in application is shown to be without compensating advantages in promoting stability.

While it is desirable that the nomenclature of the rusts should be governed by the same rules formulated for plants in general, there are two features of the rusts that so far have prevented the application of a correspondingly consistent nomenclature, both as regards species and genera. One is the status to be accredited correlated species (p. 100), and the other is the place to be given to varieties and races (p. 104). Possibly when more complete and comprehensive knowledge of the rusts is available these difficulties may so largely vanish or be so much diminished that the nomenclature may be brought into line with that of other plants.

At the present time the nomenclature problem as it applies to the rusts is in a state of flux. No author has yet consistently used generic and specific names in a manner that accords with the usage for higher plants.

TAXONOMY

In order to illustrate the biologic history of the Uredinales over 400 names of species or near-species have been mentioned in the present treatise. These numerous kinds of rusts are distributed under more than 50 genera, and sometimes they are collectively spoken of under family or subfamily names. In most instances certain relationships, community of behavior, or similarities of structure are implied, not only with other kinds which are mentioned, but with the few or many kinds which belong to the group being considered. To appreciate fully the significance of the citations of material one should not only have some knowledge of the particular kind but of its interrelationships, which in turn implies a measure of taxonomic understanding.

The taxonomy of the rusts has been undergoing changes as knowledge of their structure and behavior has accumulated. As previously indicated no generally accepted classification has yet been proposed. In the present treatise a small but significant amount of deviation from the most recent and best known systems has been admitted. In order to supply the reader with the means for interpreting this undercurrent of classification and consequent nomenclatural change, the following skeletonized key is appended, in which only the names of rusts used in other parts of this treatise are included.

There are four features in which the classification here presented differs from that used in the North American Flora (p. 108), which in turn was modified from that by Dietel (p. 107).

(1) The internal formation of the basidium should no longer be recognized as a character of dominant value, "but as an independently acquired adaptation" (Dietel, 1922), a conclusion that has been reached by comparative study showing that genera brought together by this character have diverse relationships. The family of the Coleosporiaceae has, therefore, been suppressed, and the genera under it distributed in the other two families: the Melampsoraceae (Uredinaceae) and Pucciniaceae (Aecidiaceae).

(2) The character of the life-cycle is not made a rigid criterion for the separation of genera. In some instances, however, microcyclic forms are retained under generic names distinct from those of their correlated macrocyclic forms. This is done as a matter of convenience, and consequently is not uniform. Thus, while Gallowaya, Necium, Kunkelia, Polythelis and Endophyllum are retained, yet Teleutospora and Micropuccinia are not. It is an arbitrary choice, to be considered as a temporary expedient in the interest of clarity until such time as a

more intimate understanding of the rusts permits of a more acceptable generic classification and corresponding nomenclature.

(3) In separating the two families of the rusts it is recognized that some of the genera with sessile and sometimes catenulate teliospores, *e.g.*, Cerotelium, Aplopsora, Ochropsora and Phakopsora, have other characters that show their greater relationship to Pucciniaceae rather than to Melampsoraceae. Furthermore such genera, while forming more or less waxy telia, do not have teliospores that are grown together laterally (Dietel, 1923), as in the Melampsoraceae.

(4) The strict application of the principle of priority has been abandoned, and names in general use and widely known are retained, rather than the less known names of earlier date. Thus, *e.g.*, Puccinia and Uromyces are accepted in place of Dicaeoma and Nigredo. This is done with the hope that sometime such a departure will have the sanction of an authorized committee on *nomina conservanda*. The same may be said of some specific names, *e.g.*, *Puccinia graminis* is adopted instead of the older name, *P. poculiformis*. Such exceptions to an admirable rule are reluctantly but advisedly made in order to facilitate the recognition of the objects to which reference is made. Fortunately scarcely five per cent of all generic names among the Uredinales, or one per cent of the specific names, are thus affected, and rarely will such divergence be noticed by others than technical students of the subject.

The present treatise recognizes an expansion of the genus Gymnotelium to include species with cupulate aecia which heretofore have been placed under Gymnosporangium. This is done, among other reasons, to emphasize the differences between cupulate and cornute aecia (p. 134), and to place less stress upon the presence or absence of uredinia as generic characters. The consequent transfer of species from Gymnosporangium to Gymnotelium necessitates two new combinations, for which the senior author stands sponsor, *Gymnotelium blasdaleanum* (Dietel & Holway) and *G. myricatum* (Schw.).

Another innovation, which has slowly been taking place in mycologic writings, is the recognition of a trinomial to indicate races (p. 253). Thus *Puccinia graminis* is separable into *P. gr. tritici, bromi, secalis, avenae, phlei-pratensis*, etc., *Puccinia rubigo-vera* into *P. r.-v. tritici, bromi, secalis, tomipara*, etc., *Puccinia glumarum* into *P. gl. tritici, hordei, secalis, elymi, agropyri*, etc., *Uromyces trifolii* into *U. tr. fallens, hybridi, trifolii-repentis* and *Uromyces appendiculatus* into *U. app. phaseoli, vignae*. Many other species are now known to be similarly

separable, and others will be found as physiologic studies are extended.

In the following key the microcyclic genera are placed in parentheses directly after the genera with which they are correlated.

Uredinales Mentioned in the Present Treatise

Melampsoraceae: Telia with sessile teliospores, compacted into layers or columns, and united laterally.

I. **Pucciniastreae.**
- Uredinopsis.
- Milesia.
- Hyalopsora.
- Pucciniastrum.
- Calyptospora.
- Melampsorella.
- Melampsoridium.

II. **Cronartieae.**
- Cronartium.
- Crossopsora.
- Melampsoropsis (Chrysomyxa).
- Coleosporium (Gallowaya).
- Melampsora (Necium).

Pucciniaceae: Telia with pedicelled or sessile teliospores, free or fascicled, but not united laterally.

I. **Ravenelieae.**
- Ravenelia.
- Cystomyces.
- Uromycladium.
- Hemileia.
- Cystopsora.
- Pileolaria.
- Tranzschelia (Polythelis).

II. **Phragmidieae.**
- Phragmidium.
- Xenodochus.
- Earlea.
- Trachyspora.
- Triphragmium (Nyssopsora).
- Frommea.
- Gymnoconia (Kunkelia).
- Kuehneola.
- Spirechina.

III. **Uropyxideae.**
- Uropyxis.
- Prospodium.
- Olivea.
- Cerotelium.
- Aplopsora.
- Ochropsora.
- Phakopsora.

IV. **Aecidieae.**
- Desmella.
- Calidion.
- Puccinia (Endophyllum).
- Uromyces.
- Sphenospora.
- Gymnotelium.
- Gymnosporangium.

V. **Dasysporeae.**
- Dasyspora.

In addition to the above Goplana, Maravalia, Chrysopsora, Diorchidium, Ctenoderma and Botryorhiza, all microcyclic genera, are not placed in the key, but evidently belong among the Pucciniaceae. There are also in addition the form-genera Peridermium and Roestelia belonging to the Melampsoraceae and Pucciniaceae respectively, and also Uredo, Aecidium and Caeoma belonging largely in the latter family.

CHAPTER IV

CYTOLOGY AND MORPHOLOGY

Mycelium and haustoria: distribution; protoplasmic contents; mode of division; changes during mitosis; penetration of the host-cell; formation of the haustorium.

Nuclear history: fusion of cells; two theories of sexuality; fusion of nuclei; stages in mitotic division; number of chromosomes; the nucleolus; second mitotic division.

Sori and spore-forms: pycnia, definite and indefinite forms; cupulate aecia, formation and changes of the primordium, hymenium, sporulation; cornute aecia, course of development; operculate aecia, one corticolous and two foliicolous forms; naked aecia, primordium scant; stylosporic aecia, spores arise by budding; hyphoid aecia; uredinia, similar or unlike the aecia that precede, paraphyses and peridia; telia, pedicellate and sessile teliospores; microtelia, three categories, prehymenial fusions.

Abnormal development: multiple nuclei; uninucleate races; binucleate races without nuclear fusion.

MYCELIUM AND HAUSTORIA

The mycelium originates from the germination of a spore. The germ-tube either enters through a stoma, as with most aeciospores and urediniospores, or by direct puncture of the cuticle and wall of the epidermis, as with most basidiospores. By either method there is frequently considerable swelling of the germ-tube before entry into the host, forming the appressorium, and immediately after entry, forming the substomatal or subepidermal vesicle.

The course of the mycelium within the tissues of the host is almost entirely intercellular. The hyphae are usually abundant and conspicuous in affected parts. They occur in all tissues of the leaf, and are especially abundant in the spongy mesophyll, but in stems, particularly those of woody plants, they may be restricted to certain tissues, as is true of some species of Peridermium and Gymnosporangium. The hyphae are fairly uniform in diameter, and measure about 5μ as a rule, but marked variations occur. Septation takes place with considerable regularity, and the length of the cell is usually about three or four times the breadth. Branching occurs freely and is of the monopodial type.

The cytoplasm of the hyphal cell is dense and homogeneous at first, becoming more or less vacuolate at maturity. The nucleus is moderately large (Fig. 53 *n*). It contains a clearly defined nucleolus and a network of chromatin, which is oriented or attached at a point on the

nuclear membrane. A central body, or centrosome, is thought to occur at this point of attachment, but it is not clearly seen on the resting nucleus. The hyphal cells are of two kinds with regard to nuclear content: those of the haploid mycelium having a single nucleus (Fig. 53 *A*), and those of the diploid mycelium containing two nuclei, constituting the dikaryon (Fig. 53 *B*).

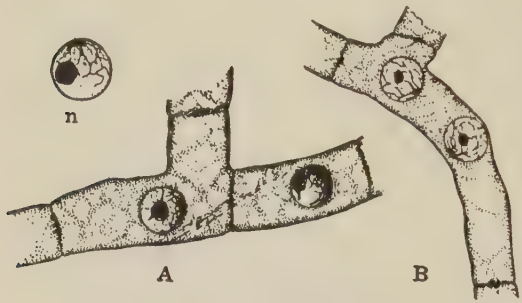


FIG. 53. — Cells of haploid and diploid mycelium: *A* two cells of the haploid mycelium of *Cronartium ribicola* from Pinus; the nucleus in each cell contains a central nucleolus, chromatin network, and a centrosome which is attached at one side to the nuclear membrane, to which the chromatin fibers converge. Details are better shown at *n*. *B* one cell of the diploid mycelium of same species from Ribes; each of the conjugate nuclei shows a nucleolus, chromatin network and laterally attached centrosome. (After Colley, 1918.)

There is no essential difference between the nuclear behavior in the uninucleate cells of the gametophyte and the binucleate cells of the sporophyte. When the dikaryon of the latter divides the two conjugate nuclei act independently, but almost or quite simultaneously. Each nucleus forms its own spindle, the spindles remaining separate throughout the process. The spindles may be oriented differently in the beginning, but they soon come to lie in the same plane, with their long axes parallel to the long axis of the cell. Subsequent formation of a wall separates the four nuclei produced by the division of the dikaryon in such a manner that the two nuclei in each of the resulting cells are never sister nuclei.

FIG. 54.—Dumb-bell shaped nuclei seen during the formation of the basidium of *Coleosporium sonchi*. (After Sappin-Trouffy, 1896.)

Earlier workers, especially those who studied the dikaryon, considered all nuclear phenomena in the vegetative cells of the rusts to be of the nature of direct division. The presence of two-parted, dumb-bell shaped masses (Fig. 54) in the later stages of mitosis, anaphase and telophase, were interpreted as representing but two chromosomes or one longitudinally split chromosome. This appearance and consequent interpretation was probably due to poor fixation. No convincing evidence has yet been produced to indicate the existence of amitosis or direct division in the rusts.

Contact between the mycelium of the rust and the nutritive substances of the host-cell, enabling the fungus to secure its nourishment, is effected by haustoria, which are variable in form and often distinctive in different species of rusts. They range in form from small knobs (Fig. 55 *A*) and elongated sacks (Figs. 1 *b* and 55 *B*) to cylindric, spiral or branched extensions (Fig. 55 *C*), sometimes proliferating as botryose structures, *e.g.*, in *Gymnoconia interstitialis* (Clinton, 1893), *Botryorhiza hippocrateae* (Olive, 1918) and in Uredinopsis and Milesia (Moss, 1926), and may at times completely fill the host-cell (Tischler, 1911). The haustoria may now and then be so evident and distinctive as to be useful in diagnosis, as in *Cronartium ribicola* (Colley, 1918).

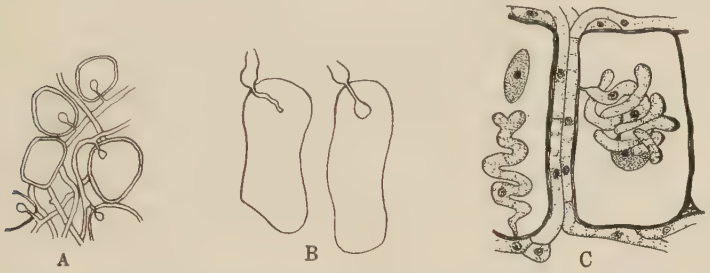


FIG. 55. — Forms of haustoria: *A* in *Hemileia vastatrix*, *B* in *Cystopsora oleae*, both tropical rusts of Asia and Africa, *C* in *Puccinia violae*, partly inclosing the nucleus of the cell. (*A* after Sydow, 1902–04; *B* after Butler, Ann. Myc. **8** : pl. 6; *C* after Sappin-Trouffy, 1896.)

In systemic invasion of the host the mycelium penetrates between the closely packed meristematic cells of the growing point, but no haustoria are developed until the cells of the organ become vacuolated and are separated by intercellular spaces (Tischler, *l.c.*).

It is the rule to find but one haustorium in any one cell of the host, but sometimes there are more and as many as ten do occasionally occur with *Gymnosporangium fraternum* (Dodge, 1918a). The fully developed haustorium frequently lies in close proximity to the nucleus of the host, and sometimes surrounds it and even appears to indent it.

The plasma membrane of the host-cell is not at first penetrated by the haustorium, but on the contrary appears to be merely invaginated and pushed inward by the growing tip (Colley, 1917b; Allen, 1923a). It is probable that in no instance does the haustorium come into organic contact with the protoplasm of the host-cell. At times a sheath forms about the base and over the tip of the haustorium (Fig. 56) consisting of

the same substance as the walls of the mycelium. Such a sheath sometimes encloses the whole haustorium.

The haustoria are formed in a definite and regular manner in the few species in which the process has been studied. In the wheat plant, invaded by the uredinial mycelium of *Puccinia graminis* (Allen, 1923a) the tip of a hypha forms a short terminal cell at any point where growth is impeded by the cells of the host. This terminal cell is a haustorium initial and contains the same number of nuclei as the other cells of the mycelium from which it is derived. It expands somewhat and gives rise to an exceedingly fine outgrowth, which penetrates the host-cell. After entering the host-cell it again expands and the cytoplasmic and nuclear contents of the initial portion pass into the part within the host-cell.

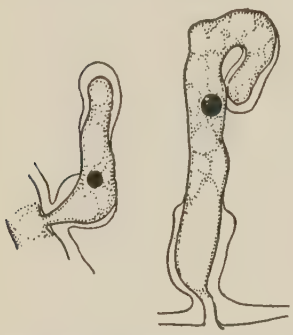


FIG. 56. — Haustoria of *Cronartium ribicola* with sheath formed about the base and over the tip. (After Colley, 1918.)

NUCLEAR HISTORY

Nuclear association to form a dikaryon, which is usually considered the first step in the fertilization of the rusts, is brought about by the fusion of two cells into the so-called fertile cell, which usually functions directly as a sporophore or basal cell. The two cells, or "gametes," which unite to form the fusion cell, are similar in all essential features, and are but slightly differentiated, if at all, from adjacent cells. The two cells that fuse are usually shorter and broader than the other cells of the hyphae and have a denser cytoplasm and larger nuclei, but they have no other features which would clearly distinguish them as "gametes."

The position of the fusing cells with reference to each other is somewhat variable. They are usually formed within the aecial or microtelial primordium as a rather definite palisade with their long axes perpendicular to the epidermis of the host. The union occurs commonly between cells which lie side by side with their lateral walls in contact (Fig. 57 *a*, *b*). The cell-walls are absorbed at the points of contact, and the resulting fusion cell is readily recognized as a double cell, the product of two equal "gametes." The fusion cell elongates considerably and later abstricts the spores. A double base can sometimes be recognized even after sporulation begins, in other cases the union of the two

cells may be so complete as to obscure this feature. This type of union, which has been called equal-cell fusion, was first described by Christman (1905a) in the caeomoid aecium of *Earlea speciosa* (*Phragmidium speciosum*). It has now been demonstrated in the majority of species that have been studied.

Another type of cell union, which differs from equal-cell fusion chiefly in matter of degree, has been designated as nuclear migration (Fig. 58 *a*, *b*). This process was first described by Blackman (1904) in *Phragmidium violaceum*, a species with caeomoid aecia, and it has been recorded since in a few additional species. As first described by Blackman the nucleus of one cell passed into the other through a minute pore which was not visible before or after the passage. Welsford (1915) reinvestigated this species and found that the pore is relatively large in some instances, so that the nucleus is not noticeably constricted in passing, and that the pore in such instances can be seen after its passage.

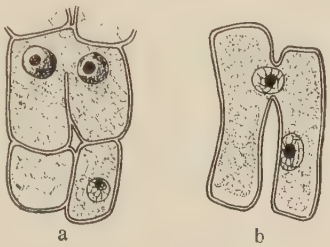


FIG. 57. — Equal-cell fusion in aecium of *a Pucciniastrum myrtilli*, *b Cronartium pyriforme*. The nucleus is passing over from one cell into the other in the latter instance. (After Adams, 1919.)

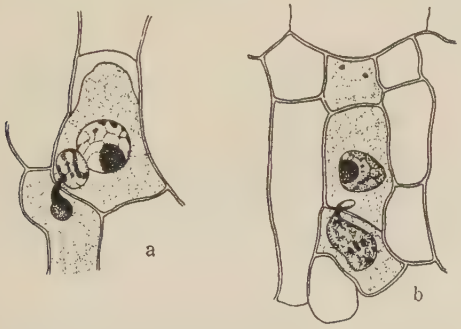


FIG. 58. — Nuclear migration in *Phragmidium violaceum*: *b* early stage with the nucleus of the lower cell beginning to pass into the cell above; *a* later stage when the nucleus of the lower cell has almost entirely passed into the upper cell. (After Blackman, 1904.)

The cell into which the nucleus migrates is usually slightly above the other, and the upper cell then functions as a basal cell. Sometimes the two cells are in the same hypha, and in such cases it is possible that the migration of the nucleus is due to some traumatic condition. Fertilization stages recognizable as nuclear migrations and as equal-cell fusions have in a few instances been described from the same species of rust (Olive 1908a; Pavolini, 1910; Kursanov, 1915, 1922; Lindfors, 1924), and it seems evident that there is no essential difference between the two processes.

However, theories as to the origin and nature of sexuality in the rusts

have been founded upon these two ways of forming the dikaryon. One theory, first announced by Blackman (1904), considers the process to be a substitute for a pre-existing oögamous type in which the female cell, the "gamete" into which the nucleus migrates, was fertilized by the pycniospore. Another theory originated by Christman (1905a) considers the process to be isogamous and the pycniospores to be conidia of the gametophyte which have become functionless.

The two theories have received such prominence that it seems well to bring together the data upon which they are founded, which is done in Table 6. Kursanov (1915, 1922) has elaborated a different view regarding fertilization in the rusts. He does not believe that there is

TABLE 6 — FORMS OF CELL FUSION

The species are grouped according to life-cycles and kinds of sori. Nuclear migration is indicated by the letter *m*, and equal-cell fusion by the letter *e*.

	Species	*Host*	*Fusion*	*Investigator*	*Date*
		MACROCYCLIC RUSTS			
		Aecia cupulate, i.e., aecidioid			
Uredinia present	Uromyces poae	Ranunculus ficaria	*m*	Blackman & Fraser	1906
	Uromyces dactylidis		*m, e*	Pavolini	1910
	Uromyces scirpi	Hydrocotyle umbellata	*e*	Fromme	1914
	Uromyces caladii	Arisaema triphyllum	*e*	Fromme	1914
	Puccinia poarum	Tussilago farfara	*m*	Blackman & Fraser	1906
	Puccinia angustata	Lycopus virginicus	*e*	Fromme	1914
	Puccinia eatoniae	Ranunculus abortivus	*e*	Fromme	1914
	Puccinia violae	Viola papilionacea	*e*	Fromme	1914
	Puccinia caricis	Urtica sp.	*e*	Kursanov	1915–22
Uredinia none	Puccinia falcariae	Falcaria rivini	*e*	Dittschlag	1910
	Puccinia claytoniata	Claytonia virginica	*e*	Fromme	1914
	Puccinia tragopogi	Tragopogon sp.	*e*	Lindfors	1924
		Aecia cornute, i.e., roestelioid			
Uredinia none	Gymnosporangium bermudianum	Juniperus virginiana	*e*	Thurston	1923
		Aecia operculate, i.e., peridermioid			
Uredinia present	Coleosporium sp.	Pinus sylvestris	*e*	Kursanov	1915–22
	Coleosporium solidaginis	Pinus rigida	*e*	Adams	1919
	Coleosporium euphrasiae	Pinus sp.	*e*	Lindfors	1924
	Pucciniastrum myrtilli	Tsuga canadensis	*e*	Adams	1919
	Uredinopsis mirabilis	Abies balsamea	*e*	Adams	1919
	Cronartium ribicola	Pinus strobus	*e*	Colley	1918
	Cronartium comptoniae	Pinus virginiana	*e*	Adams	1919
	Cronartium pyriforme	Pinus pungens	*e*	Adams	1919

	Species	Host	Fusion	Investigator	Date
		Aecia naked, i.e., caeomoid			
Uredinia present	Phragmidium violaceum	Rubus fruticosus	*m*	Blackman	1904
	Phragmidium violaceum	Rubus sp.	*m*	Welsford	1915
	Phragmidium disciflorum	Rosa sp.	*e*	Moreau	1914
	Melampsora rostrupii	Mercurialis perennis	*e*	Blackman & Fraser	1906
	Melampsora lini	Linum usitatissimum	*e*	Fromme	1912
	Melampsora reticulata	Saxifraga aizoides	*e*	Lindfors	1924
Uredinia none	Phragmidium speciosum	Rosa humilis	*e*	Christman	1905a
	Gymnoconia interstitialis	Rubus sp.	*m, e*	Olive	1908a
	Gymnoconia interstitialis	Rubus sp.	*m, e*	Kursanov	1910
		Aecia stylosporic, i.e., uredinoid ("primary uredo")			
Pycnia present	Frommea obtusa	Potentilla canadensis	*e*	Christman	1907a
	Triphragmium ulmariae	Ulmaria rubra	*m, e*	Olive	1908a
	Triphragmium ulmariae	Ulmaria sp.	*m, e*	Kursanov	1915–22
	Triphragmium ulmariae	Ulmaria sp.	*m, e*	Lindfors	1924
	Trachyspora alchemillae,*	Alchemilla subcrenata	*m, e*	Kursanov	1915–22
	Trachyspora alchemillae,*	Alchemilla sp.	*m, e*	Lindfors	1924
	Puccinia suaveolens	Cirsium arvense	*m*	Kursanov	1915–22
		MICROCYCLIC RUSTS			
		Microtelia aecidioid			
Pycnia present	Endophyllum sempervivi	Sempervivum sp.	*e*	Hoffmann	1911
		Microtelia hyphoid			
Pycnia none	Chrysomyxa abietis	Picea sp.	*e*	Kursanov	1915–22
	Chrysomyxa abietis	Picea sp.	*e*	Lindfors	1924
	Gallowaya pinicola	Pinus virginiana	*e*	Dodge	1925
		Microtelia puccinioid			
Pycnia none	Puccinia malvacearum	Malva sylvestris	*e*	Werth & Ludwigs	1912
	Puccinia buxi	Buxus sempervirens	*e*	Moreau	1914
	Puccinia morthieri	Geranium sp.	*e*	Lindfors	1924
	Uromyces ficariae		*e*	Moreau	1914
Pycnia present	Uromyces scutellatus	Euphorbia virgata	*e*	Kursanov	1915–22
	Puccinia rossiana	Scilla cernua	*m*	Kursanov	1915–22
	Puccinia transformans	Tecoma stans	*e*	Olive	1908a
	Polythelis fusca	Anemone sp.	*e*	Pavolini	1912
	Polythelis fusca	Anemone nemorosa	*m, e*	Lindfors	1924

* Pycnia unknown, but doubtless occur under favorable conditions.

sufficient reason to consider the cells which unite as essentially different from other cells of the mycelium, but thinks that such differences as they sometimes possess are due to their position, and are not constitu-

tional. According to his view, fertilization in the rusts is essentially an apogamous process, or a pseudomyxis. Other opinions regarding fertilization in the rusts are more or less variants of these three views.

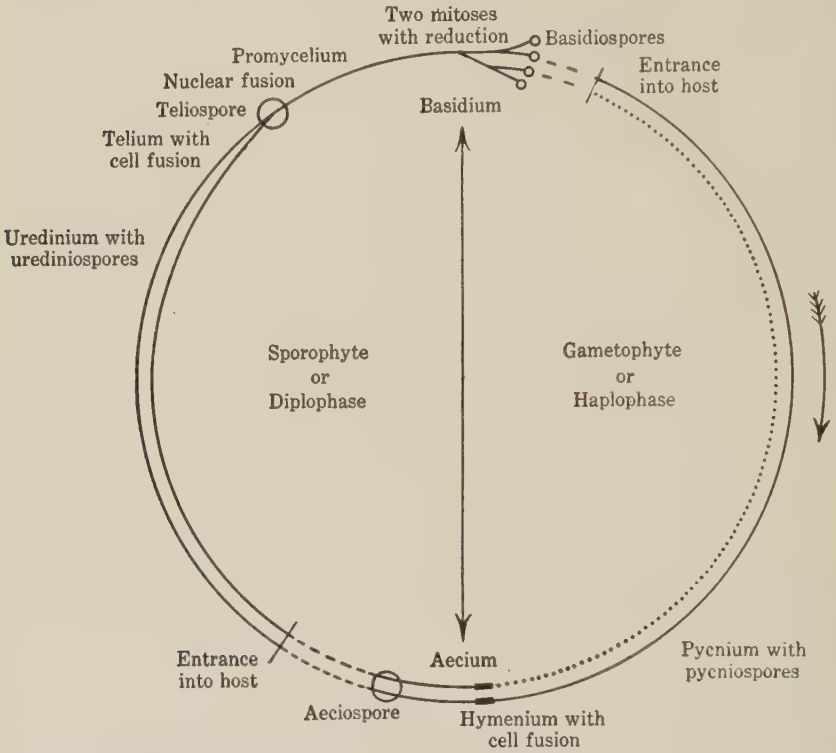


Fig. 59. — Diagram to show the nuclear course in the life-cycle of a macrocyclic rust in full normal development: the solid lines represent the course of individual nuclei. The interrupted lines show passage of spores through the air. The dotted line shows the hypothetical course of one of the conjugate nuclei, as presumably derived from one of the pairs of the four basidiospores which supplies its associated nucleus from a similar source (heterothallic). The two conjugate nuclei may be conceived to come from one basidiospore (homothallic), which would require that the dotted line in the diagram be omitted. The origin and course of the associated nuclei are not definitely known. (Original.)

The association of two nuclei in a cell, which appears to constitute the beginning of the process of fertilization in the rusts, both macrocyclic (Fig. 59) and microcyclic (Fig. 60), takes place at or near the end of the gametophytic phase of the life-cycle, and yet the fusion of the conjugate nuclei does not occur until the teliospore is reached. The two nuclei in each cell of the young teliospore approach each other as the

spore matures. When they come together the nuclear membranes disappear at the points of contact, and the contents are free to mix. The fusion nucleus soon rounds up and the membrane is reorganized around the whole. Evidence of the double origin is seen in the presence of two nucleoli, which persist for a while. A marked increase in size occurs at this time (Fig. 61), and this enlargement may continue until the volume of the fusion nucleus may be as much as four times the combined volume of the two contributing nuclei (Colley, 1918). Shortly after this union is accomplished, nuclear division takes place after a mitotic fashion more or less similar to what occurs in other plants, accompanied with a redistribution of the chromosomes.

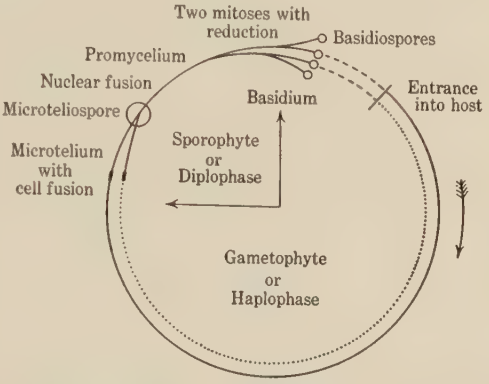


FIG. 60. — Diagram to show the nuclear course in the life-cycle of a microcyclic rust. (Original.)

All the stages of typical mitotic division have not been demonstrated, but the essential details of the process have been seen (Fig. 62). As a

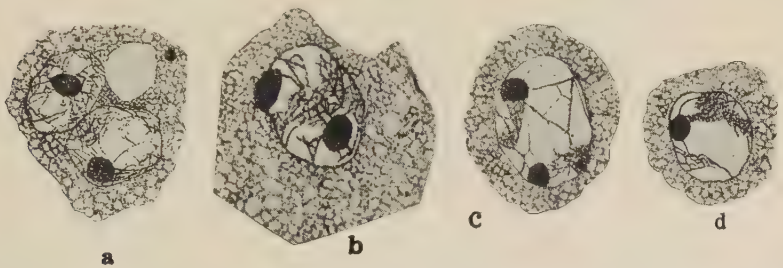


FIG. 61. — Fusion of nuclei in the teliospore of *Coleosporium solidaginis:* *a* the conjugate nuclei ready to fuse, *b* shortly after fusion has taken place, the nucleus much enlarged, *c* later stage with the two nucleoli still separate, *d* nucleus returned to the resting stage, the two nucleoli having fused. (After Holden & Harper, 1903.)

preliminary to the first division the nucleus enlarges considerably and a clearly differentiated spindle is formed on one side of the nuclear membrane between the two centrosomes (Fig. 62 *A f*), which are presumed to have been derived by the division of a single centrosome of the resting nucleus. The nuclear membrane breaks down and disappears at this

stage, and the chromosomes seen as rounded or slightly elongated bodies are drawn against the spindle by kinoplasmic threads which are some-

Fig. 62. — Mitotic division of the nucleus to form the basidium: *A* in *Cronartium ribicola; b* basidiospore after nuclear fusion has taken place, showing centrosome at one side of the nucleus, *f* early prophase, showing chromatin threads, *g* later stage, *h*, *i* early anaphase with distinct chromatin connecting fibers and an indefinite equatorial plate, *j*, *k* still later anaphase with chromosomes well advanced toward the poles, the polar radiations indistinct; *l* late anaphase, chromosomes in two groups, polar radiations distinct; *B* in *Coleosporium solidaginis; a* fusion nucleus, *b* early prophase, *c* somewhat later prophase, *d* early equatorial plate stage, *e* later stage, *f* anaphase showing chromosomes grouped about the poles, with polar radiations. (*A* after Colley, 1918; *B* after Holden & Harper, 1903.)

times visible. A rather indefinite spireme is formed in earlier stages. The equatorial-plate stage (Fig. 62 *A h, i, B d, e*) is not clearly defined, but chromosomes in a mass at the center of the spindle can be seen

(Holden & Harper, 1903; Colley, 1918), which may represent this stage. In the separation of the mass into two groups preliminary to passing to the poles sixteen chromosomes are distinguishable in *Cronartium ribicola*, and each daughter nucleus apparently is reconstructed around a group of eight chromosomes.

The exact numbers of chromosomes in the rusts are difficult to determine because they are very small and poor fixation of mitotic figures commonly occurs. In the first division of the fusion-nucleus in the basidium of *Coleosporium solidaginis* (Holden & Harper, 1903) the number appears to lie between six and ten, while in other species of Coleosporium it has been determined as eight (Moreau, 1914). In the anaphases of uninucleate hyphae and cells of the pycnium of *Triphragmium ulmariae* eight chromatin masses, interpreted as chromosomes, are seen at each pole (Olive, 1908a). These are considered as haploid numbers and the two divisions of the fusion nucleus are regarded as comparable to the heterotypic and homotypic mitoses of the higher plants. In *Puccinia arenariae*, however, eight chromosomes are seen at the center of the spindle and four pass to each pole (Lindfors, 1924). In the second division four chromosomes are also seen at each pole and the haploid number in this species appears to be four.

In the telophases of mitosis the individual chromosomes are usually not distinguishable but appear as a two-parted, lobed mass at each pole (Fig. 62 *B f*). There is no clear explanation for this separation into two masses, although it may result because of a preliminary division of the centrosome (Olive, 1908a). Definite polar radiations are seen in the later stages of mitosis, but they are invisible or are seen with difficulty in earlier stages.

The nucleolus, which is cast aside at the beginning of mitosis, persists during the process as a less and less definite body and finally disappears (Walker, 1927). A nucleolus appears *de novo* in each of the daughter nuclei.

The second mitosis, which is required to complete the formation of the four cells of the basidium, is not so well defined as in the first mitosis, and is more difficult to follow.

The reduction division which the fusion nucleus undergoes in the basidium, as just described, completes the nuclear history. Fertilization was initiated by cell fusion at the beginning of the dikaryon, followed in due course of time by fusion of the conjugate nuclei in the teliospore, and the cycle is completed by reduction of the chromosomes during mitoses in the formation of the basidium.

SORI AND SPORE-FORMS

Pycnia and pycniospores. — The pycnia are usually produced shortly before or simultaneously with the aecia or microtelia, and are borne on the same mycelium. In certain species, however, a considerable interval may elapse between the formation of the two fructifications. In *Hyalopsora aspidiotus* and *Cronartium ribicola*, for example, the pycnia precede the aecia by at least one growing season.

Pycnia are of two general forms: (1) flat and indefinite, either subcuticular or subcortical, often called caeomoid (Fig. 11 *a*, *b*), or (2) globular to flask-shape and definite (Fig. 11 *c*). The indefinite forms develop from a thin primordium, which differentiates into a flat hymenium extending centrifugally with no outer boundary except tissues of the host. In the subcortical or crust-like forms (Fig. 11 *b*), which arise between the thin-walled cork and the underlying cortical parenchyma, they may reach ten or fifteen millimeters in length and may have nearly the same breadth, but in the subcuticular and subepidermal forms they are usually much less than a millimeter in diameter.

The pycnial hymenium consists of a palisade of sporophores, upright in indefinite forms and converging in most of the other forms. The sporophores are either rod-like (Fig. 12 *A*) or tapering upward (Fig. 12 *B*) and are either single or branched. The pycniospores are successively produced at the tips of the sporophores as buds which enlarge to full size and are then separated by constriction. The nucleus of the sporophore divides, and one of the daughter nuclei passes into the young pycniospore (Fig. 12 *A*). The pycniospore is detached by the formation of a new bud beneath, and the process is repeated a number of times. The pycniospores accumulate above the hymenium, and together with a sweet secretion are discharged into the air through longitudinal slits in the overlying tissues, as in most coniferous rusts, or through irregular or pore-like openings, as in most angiospermous rusts.

The definite forms have a more or less globoid primordium, the middle portion developing into a curved hymenium and the sides into overarching paraphyses (Fig. 11 *c*). The sporophores converge toward the center of the pycnium and discharge their spores into the central cavity. The paraphyses or sterile sporophores become longer toward the upper part, and extend in a hollow column beyond the surface of the host, forming an ostiole through which the spores and sweet liquid are discharged. In a few globoid pycnia, *e.g.*, in the genus Milesia, protruding paraphyses are wanting (Fig. 63).

The pycniospores may be globoid, ellipsoid or pyriform, and are small,

generally from 3 to 5μ in the longer diameter. The nucleus is relatively large in comparison with the spore and the cytoplasmic contents are scanty. Nucleoli are lacking, or if formed are minute. Apparently the spores contain little or no reserve food to promote growth. They do not germinate in water, and show no extended germination in nutrient solutions. Repeated attempts to infect the host with them have been unsuccessful (Plowright, 1889; Klebahn, 1899), but they may exert a quickening influence upon the development of the aecia (Craigie, 1927b).

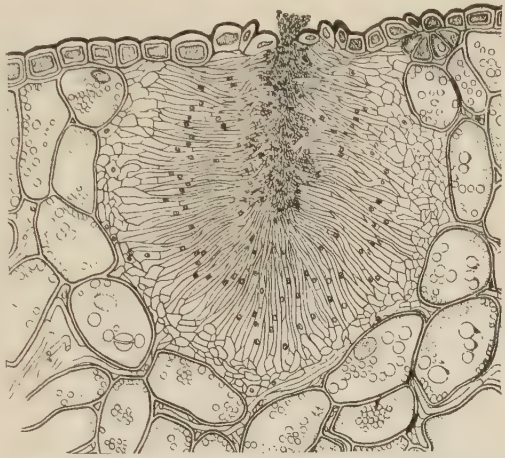


Fig. 63. — Subepidermal pycnium of *Milesia marginalis* on *Abies balsamea;* paraphyses wanting. (After Hunter, Bot. Gaz. **83** : pl. 11.)

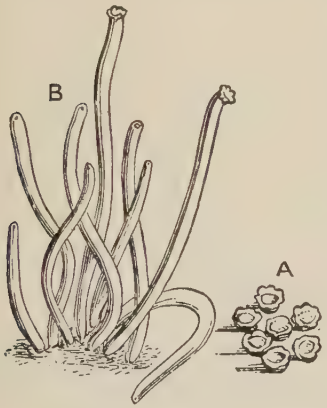


Fig. 64. — Aecia of *Puccinia graminis* grown by Plowright on Berberis: *A* normal appearance, *B* elongated form; both with same magnification. (After Worthington G. Smith, Gard. Chron. **22** : 308.)

Aecia and aeciospores. — It is a safe generalization that all aecial forms, however diverse in appearance, start with a primordium differing only in size and contour, and pass through a similar set of changes to reach the mature form. The differences are chiefly those of elaboration. Of the several forms of aecia, *i.e.*, (1) cupulate, (2) cornute, (3) operculate, (4) naked, (5) stylosporic and (6) hyphoid, the first or cupulate form is not only the best known and most commonly met with, but shows well the several successive steps of development.

(1) *Cupulate aecia.* — The designation is due to the cup-like appearance of the sorus when mature and open for the spores to be shed (Fig. 13). In many species it suggests a white cup with flaring brim filled with golden-yellow powder. When the atmosphere is

dry and still during growth the sides of the cup may be extended into a cylinder two to many times the diameter (Fig. 64).

The cupulate aecium when mature consists of a peridium, one cell in thickness throughout and usually colorless, with a hymenium at base giving rise to chains of more or less isodiametric spores separated by intercalary cells which usually soon disappear. It is with few exceptions definite in form and development, although this is not primarily due to the restricting presence of a peridium, but rather to the enveloping hyphae which limit the lateral extension of the hymenium. In some species, *e.g.*, *Puccinia stipae*, the aecia of which occur on asters and other composites, the cells of the peridium are loosely held together and quite evanescent, while in other species, *e.g.*, *Puccinia hemispherica* on Lactuca, no peridium is present, and yet in both sorts the same definite form of the sorus is maintained.

The aecial primordium is initiated by a conspicuous massing of the gametophytic hyphae between certain cells of the host (Fig. 2). In *Puccinia claytoniata* (Fromme, 1914), which at present is one of the cytologically best known forms, the region to be included in the sorus involves about four host-cells in breadth and three in depth. The aggregated and entwisted hyphae multiply and ramify between the cells and force them apart. After the host-cells have been completely isolated from their neighbors in this manner they gradually diminish in size, and in most cases eventually disappear. In the early development the hyphae are intertwined without order, but later those in the interior of the globular mass are seen to converge toward the upper center of the primordium, while those on the boundary form a felted layer which encircles and delimits the primordium.

A differentiation of the primordium into sterile and fertile areas begins to show at an early stage. In the lower half or third of the central part the protoplasm of the hyphae becomes more dense and stains more strongly (Fig. 5), and thus indicates the fertile area in which the hymenium will be formed. The fertile area in *Puccinia claytoniata* is composed of rather uniform cells, above which is the sterile area with the cells of the hyphae becoming vacuolate and disorganized (Fig. 65). The upper area is soon transformed into the plectenchyma (also called pseudoparenchyma). As the sorus matures the plectenchyma disappears or is crushed by the developing mass of spores beneath.

The origin of the plectenchyma has been much in debate. In *Puccinia claytoniata* (Fromme, 1914) it is formed from the upper portions of the hyphae which were seen to converge toward the center of the

primordium, while the lower portions of these hyphae make up the fertile part (Fig. 65). The apical cells are the first to be differentiated and here the degeneration begins, proceeding toward the base. The cytoplasm becomes vacuolate, the nuclei are disorganized, and the cells are soon detached and greatly enlarged. The cells become closely packed together through enlargement, and the appearance of the mass in section is that of a parenchyma. This degeneration is possibly aided by a starvation phenomenon (Kursanov, 1915, 1922), the flow of nutrients through the hyphae being intercepted by the vigorous cells in the hymenium at the base. This method of formation of plectenchyma has been definitely ascertained to occur in a number of species, the extent of the change varying with the species. In some aecia which are formed deep in the host-tissue and which are surrounded by a conspicuous felting of hyphae, as in *Tranzschelia punctata* (Kursanov, 1915, 1922), the plectenchyma may be formed of the intermediate cells of those hyphae which traverse the primordium from the sides. In such cases neither the apices nor bases of these hyphae but only the middle parts are formed into plectenchyma.

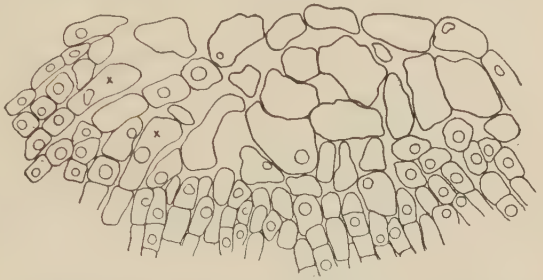


FIG. 65. — Plectenchyma in the aecium of *Puccinia claytoniata:* the continuation of the primordial hyphae into the plectenchyma is especially evident at *x*, *x*. (After Fromme, 1914.)

The lower or fertile part of the primordium undergoes changes which result in the formation of a sorus. This part may be distinguished in its early stage from the overlying plectenchyma and the bordering felt of hyphae by the density of the cell protoplasm and the general appearance of vigor. In cupulate aecia having broad bases the fertile part appears in vertical section as a crescent with the ends extending up the sides of the primordium, while in aecia having narrow bases it is restricted to a small lens-shaped mass at the base. The cells which go to form the hymenium generally fuse by pairs, and the resulting fusion cells, which are consequently binucleate, enlarge and elongate in the direction of the epidermis to form a palisade-like layer (Fig. 5) along the upper boundary of the fertile part. Practically any cell may fuse with an adjoining cell but usually only those cells in the upper boundary

layer do so. Occasionally, however, some deep-seated cells fuse and give rise to short sometimes branching chains of binucleate cells which extend into the hymenial layer, the terminal cells functioning as sporophores (Fig. 66). This is true of *Puccinia caricis* (Kursanov, 1915, 1922).

The fusion cells, which are commonly called basal cells after they begin to produce spores, constitute a sharply-defined hymenium over the floor of the sorus. The hymenium usually begins to form first in the center of the floor, and extends outward in all directions, as in *Puccinia graminis*, or it may appear to spring up over the whole floor nearly simultaneously, as in *P. caricis*. In both cases the cells at the center are likely to grow faster and arch the hymenium (Kursanov, 1915, 1922).

Fig. 66. — Part of the fertile portion in the early stage of the aecium of *Puccinia caricis* on Ribes: some of the binucleate cells originate much below the hymenium and form hyphae that terminate above and function with the other cells of the hymenium. (After Kursanov, 1915–22.)

Sporulation begins at the center of the hymenium and proceeds in a wave-like manner toward the margins, the spores being abstricted in series or chains. The longest chains are, therefore, in the center of the young aecium and those toward the margins are progressively shorter thus giving the developing mass of spores an arched appearance. In later stages the spore mass is separated from the overlying plectenchyma and the bordering hyphal felt by a peridium which forms a continuous layer one cell thick over the whole mass of spores.

The process of sporulation and of peridial formation is one of marked regularity. Each of the basal cells elongates and the upper end, approximately the upper one-third, is abstricted as a binucleate cell, which in the case of the first cell formed undergoes no further division as a rule, but is transformed into a peridial cell.

Meanwhile the basal cells have elongated again and have prepared to form spore initials. These are cut off in due time and proceed at once to an unequal division, the large upper segment becoming an aeciospore, and the much smaller lower segment forming an intercalary cell, to be considered as a rudimentary pedicel. Both segments of the spore initial are binucleate. The intercalary cells, serving as disjunctive cells, eventually become disorganized and disappear. As development

goes on in the first spore initial the basal cell beneath elongates in preparation to form a second spore initial, which in due time is cut off and undergoes similar changes to those of the first one. This process is many times repeated, each basal cell in this manner forming a chain of alternating aeciospores and intercalary cells.

The cells formed first at the ends of the aeciospore chains soon touch and adhere to form a continuous layer, which is carried upward by the increasing growth beneath, forming the dome of the peridium (Fig. 67). At the same time the peripheral circle of basal cells forms chains of cells, all of which are similar to the first cells of the central spore chains, and these adhere to form the lateral walls of the peridium. The first four or five cells of the lateral chains are scarcely distinguishable from the young spore initials of the other chains. As the transformation into characteristic peridial cells proceeds, both above and at the sides, the nuclei in them remain small or become smaller, the cytoplasm becomes thinner and more vacuolate, the outer wall of the cell increases in thickness and remains smooth but becomes more or less transversely striate while the inner wall is thinner and becomes verrucose, the whole cell usually attaining greater size. In some instances the very young peridial cells divide forming rudimentary intercalary cells. Spore-chains that are begun after the peridium forms a continuous envelope to the young sorus start with a spore initial, and not with a peridial cell, as in the earlier chains.

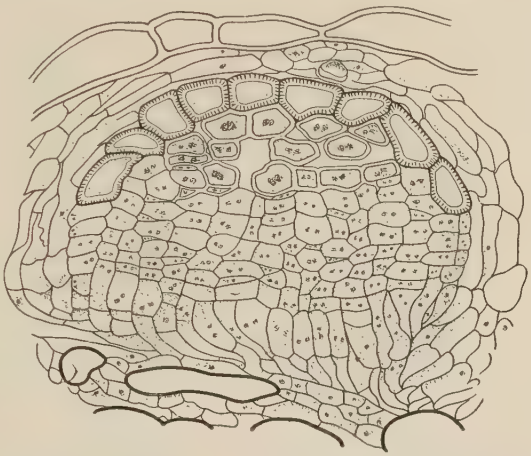


Fig. 67. — Aecium of *Uromyces poae* on Ranunculus, nearly mature: the space previously occupied by the plectenchyma is now partly filled with aeciospores, with an overarching peridium. (After Blackman, Ann. Bot. **20** : pl. 3.)

As the aecium continues to grow and mature, pressure from within causes the overlying tissues of the host to give way, and the upper part of the aecium to be extruded. The peridium then ruptures, liberating the aeciospores.

In all cupulate aecia the inner walls of the peridial cells are thin and the outer walls slightly or usually much thicker (Fig. 7). As the aecium matures, the unequally thickened walls cause the peridium upon rupturing to be reverted, in which position it remains, whether moist or dry.

Having explained the course of development of the cupulate aecium, it will not be necessary to particularize so fully in treating the other forms of aecia, but to point out wherein lie the principal differences.

(2) *Cornute aecia.* — The cornute or roestelioid aecium when mature and unruptured has a horn-like form, and is usually deeply colored, due to the dark colored spores within (Fig. 14 *a*). It is definite in form, with its long axis perpendicular to the leaf surface, and never without a peridium. The primordium is ovoid, instead of globoid as in the cupulate form (Richards, 1896; Kursanov, 1910). It usually arises deep in the mesophyll tissues of the host. The hymenium is composed of long and slender basal cells, pressed closely together (Fig. 68).

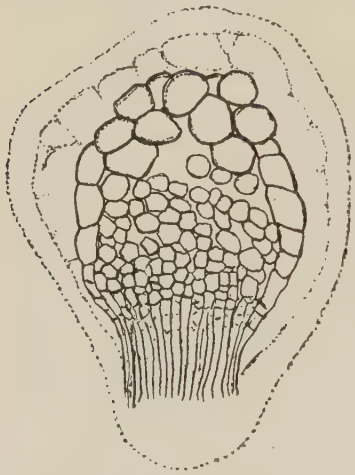


Fig. 68. — Young cornute aecium of *Gymnosporangium juniperinum* (*G. tremelloides*, *Roestelia penicillata*) showing the hymenial column of slender cells, supporting the spores, both inclosed in the large-celled peridium. The tissues of the host surrounding the aecium are partially indicated. (After Kursanov, 1915–22.)

The most exact account yet available of the course of development in the cornute aecium is that provided by Kursanov (1915, 1922), using *Roestelia penicillata* on apple leaves. This form is often placed under the name *Gymnosporangium tremelloides*, although more properly belonging under the Linnaean species *juniperinum*. In this species the primordium is composed of hyphae whose axis of growth is toward the epidermis. The plectenchyma arises as a small ellipsoid area within the central region of the ovoid primordium by the division of the hyphae into cells of nearly isodiametric proportions (Fig. 69). These cells enlarge somewhat, the protoplasm becomes less abundant, and the walls gelatinize. This gelatinization of the walls recalls the similar and very abundant gelatinization which takes place in the telium of this and other species of *Gymnosporangium*, both phenomena undoubtedly having relation to a fundamental tendency of the species which manifests itself alike in both the aecium and telium. Kursanov notes that a small

variation of the above procedure is shown in *Roestelia cornuta* on Sorbus leaves, for which species he uses the name *G. juniperinum*, instead of *G. cornutum*. In this species the additional cross walls in the primordial hyphae are not laid down, and consequently the cells of the plectenchyma remain oblong as at the beginning (Fig. 70). The degeneration of the cells and gelatinization of the walls in this species, however, proceed as described above.

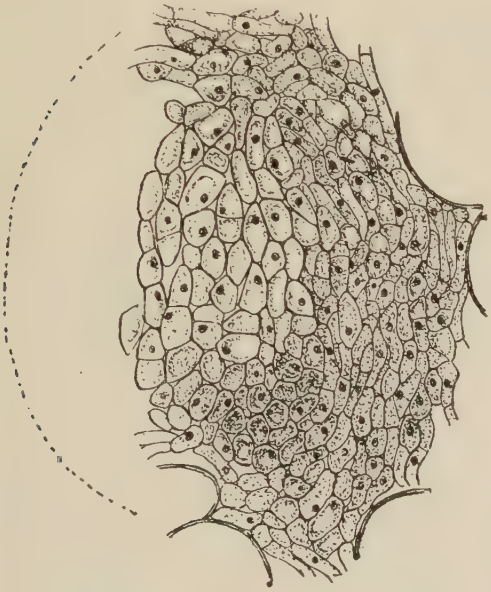


FIG. 69. — Section of the aecial primordium of *Gymnosporangium juniperinum*. The central cells have begun to deteriorate. (After Kursanov, 1915–22.)

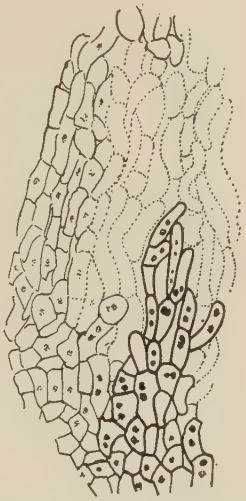


FIG. 70. — Vertical section of a part of the primordium of *G. cornutum*, (*G. juniperinum*, *Roestelia cornuta*) showing binucleate cells passing into the gelatinizing plectenchyma. (After Kursanov, 1915–22.)

Turning now to the origin of the binucleate condition in cornute aecia it is found that the first binucleate cells in limited numbers arise deep within the fertile part of the primordium and form branching rows of cells (Fig. 71), which push upward well into the gelatinous mass of disorganized cells of the plectenchyma (Fig. 70). Having penetrated a third or a half way into the plectenchyma area the terminal cells of the hyphae begin to function as basal cells, forming an indistinct hymenium. The column of binucleate hyphae, penetrating the gelatinized plectenchyma before sporulation begins, must be taken as a marked feature of cornute aecia.

The first cells cut off are at the center of the hymenium. These cells enlarge and the walls thicken, taking on the appearance of peridial cells. The central chains produce three or four such cells, decreasing to one at the edges (Fig. 72), and thus there arises a more or less conical cap. By the time the cap is well formed (Fig. 73) the other cells of the hymenium, having attained about the same level, also become active and develop chains of aeciospores and lateral peridial walls in the manner described for cupulate aecia.

FIG. 71. — Single branching row of binucleate cells from the primordium of *G. cornutum*. (After Kursanov, 1915–22.)

The peridium of cornute aecia usually differs from that of cupulate aecia by having a thickened apex, as described above. When there is an apical thickening, the rupture of the mature aecium is at the sides as longitudinal slits, forming ribbons or strings of peridial cells. Furthermore, the thickening of the walls of the cells at the sides of the peridium is the reverse of that found in the cupulate aecia, being thin on the outside and thicker, often much thicker, on the inside.

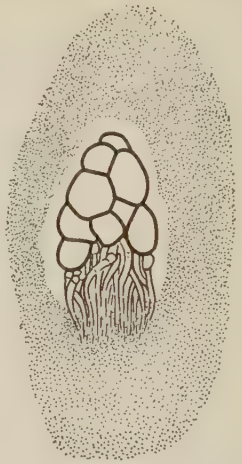


FIG. 72. — Cap formation of the cornute aecium at a later stage of the primordium of *G. cornutum*, showing the hymenial column supporting the first large cells of the peridial cap. The plectenchyma has gelatinized and disappeared. The dotted area indicates the position of the tissues of the host. (After Kursanov, 1915–22.)

A few species of Gymnosporangia, *e.g.*, *G. juniperi-virginianae*, *G. yamadae*, *G. transformans*, *G. floriforme* and *G. sabinae*, have highly hygroscopic peridia that remain open when dry, but close quickly when moistened. In such species the inner walls of the cells being thicker than the outer cause the ribbons or strings of peridial cells when moist to curl inward (Fig. 74), and thus prevent the spores from escaping.

FIG. 73. — Section through the mature peridial cap of *G. cornutum*. (After Kursanov, 1915–22.)

(3) *Operculate aecia.* — The foliicolous forms of operculate, or peridermioid aecia, are usually tongue-shaped or even cylindric (Fig. 16 *b*, *c*), while the corticolous forms are usually bullate, flat and spreading

(Fig. 16 *a*), but in a few cases inclined to be cylindric. The two sorts as a rule appear quite different, as those which occur on leaves usually cause no hypertrophy and are individualistic, while those on bark usually form galls, often of great size, and are closely associated, even becoming confluent. Their morphologic development in each case follows essentially the same course as that described for other forms of aecia, but the two sorts are distinguished to a greater or less degree by the early delimitation of the hymenium in the leaf forms and by the more indefinite extension of the hymenium in the bark forms (Adams, 1919).

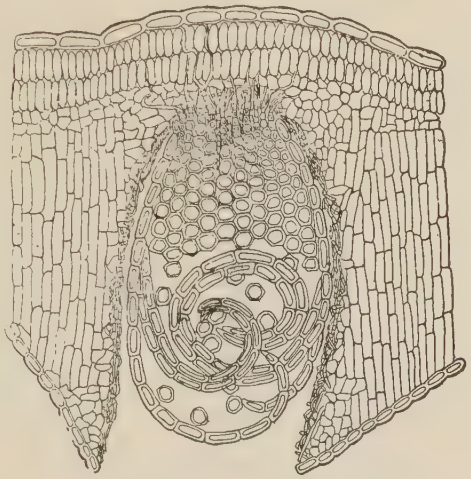


Fig. 74. — Diagrammatic drawing to show how the strings of peridial cells in the mature aecia of *Gymnosporangium juniperi-virginianae* curl inward when wet and prevent the escape of the spores. The difference in thickness of the inner and outer walls of the peridial cells is not shown. (After Lloyd & Ridgway, 1911.)

In the foliicolous species of operculate aecia, as represented by *Coleosporium solidaginis*, there are several layers of hyphae surrounding the primordium, which do not become disorganized and which serve to delimit the lateral extension of the hymenium as it develops. These felted layers are similar to those which encircle the primordium of the cupulate aecia (p. 128) and which delimit the hymenium in them, although somewhat less highly organized. Similar delimiting layers also occur in the foliicolous aecia of *Uredinopsis mirabilis* and *Pucciniastrum myrtilli*, but there appears to be no delimiting layer in caulicolous species, *e.g.*, *Cronartium pyriforme* and *C. comptoniae* (Adams, 1919).

The cells of the hymenium first become active at the center, and the production of peridial cells and spore initials continues centrifugally until the peripheral basal cells which form the boundary walls of the aecium are reached. For convenience of description and comparison operculate aecia may be separated into three sub-groups, to accord with their later development: (1) aecia belonging to the genus Coleosporium; (2) aecia belonging to the genus Cronartium; (3) aecia belonging to

the genera Uredinopsis, Hyalopsora, Milesia, Melampsoridium, Melampsorella, Melampsoropsis and Melampsora. The first and third subgroups are foliicolous and the second one corticolous.

In Coleosporium, as illustrated by *C. solidaginis* (Adams, 1919), and another undetermined species (Kursanov, 1915, 1922), the peridial initial at the distal end of the first chains cuts off its intercalary cell above (Fig. 75), but the succeeding initials, which are transformed into spores, form their intercalary cells below in the usual way. Similarly the initials of the lateral peridial walls cut off intercalary cells from the lower outer surface. The remarkable position for intercalary cells of the central chains is characteristic for the genus Coleosporium exclusively, so far as known.

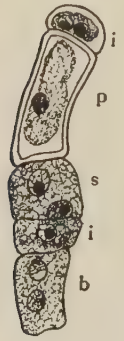


FIG. 75. — A young spore chain of *Coleosporium solidaginis* on *Pinus rigida:* the upper and oldest initial has divided to form a peridial cell *p*, and an intercalary cell *i* above, while the next initial has divided to form an aeciospore *s*, and an intercalary cell *i* below. The basal cell *b* will continue the chain. (After Adams, 1919.)

FIG. 76. — Vertical section through a young aecium of Coleosporium, showing a gelatinized outer wall *g*, bounding the hymenium and separating it from the plectenchyma above. (After Kursanov, 1915–22.)

The peridial cells of operculate aecia, both foliicolous and corticolous, by cutting off rudimentary intercalary cells (Figs. 79 and 80), show clearly in varying degree that they are transformed aeciospores. Such production of intercalary cells is a prominent but not exclusive distinction between operculate aecia and other kinds of aecia. The intercalary cells do not persist as long as those attached to spores.

In the formation of the aeciospores of Coleosporium there is a notable feature not observed in other genera. The spores in the first layer immediately beneath the operculum, upon maturing thicken the outer wall, which becomes hygroscopic and gelatinous, forming a continuous

wavy pellicle that is very marked as a colorless boundary to the spore-mass (Kursanov, 1915, 1922). This gelatinous layer in the aecium (Fig. 76 *g*) clearly corresponds in its nature to the gelatinous layer formed in the telium of Coleosporium by the well-known softening and swelling of the outer boundary walls of the teliospores. Again, as in previous cases noted, there is here shown a characteristic feature of development appearing in different parts of the cycle of the same species, or group of species.

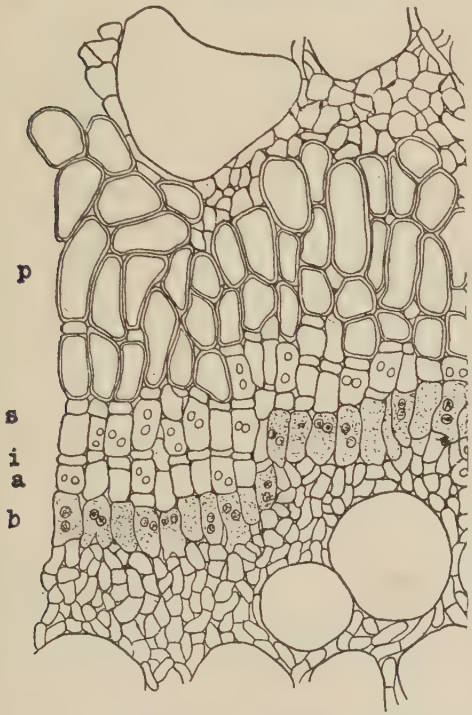


Fig. 78. — Section through the central part of the aecium of *Cronartium comptoniae* on Pinus: *b* hymenial layer; *a* aeciospore initials; *i* intercalary cells; *s* aeciospores; *p* peridial cells to form the operculum drawn with double cell-walls, some still showing their intercalary cells. (After Adams, 1919.)

The operculum attains its greatest elaboration in the genus Cronartium (Fig. 77). It ranges in thickness from

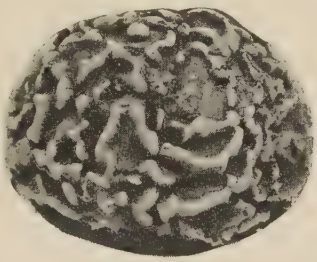


Fig. 77. — Aecia on a globoid gall of *Cronartium cerebrum* on *Pinus virginiana* before the opercula have ruptured. (Photograph by G. G. Hedgcock.)

occasionally one cell, as in *C. pyriforme* (Adams, 1919) to ten cells in *C. ribicola* (Kursanov, 1915, 1922), or even more in *C. harknessii*. In the form of the last species called *stalactiforme* there are projections from the dome that reach well down into the aecium, while in the form called *filamentosum* there are numerous uneven fibers that extend from dome to base, both being composed of sterile elements like the dome of the peridium. The development of these forms has not been studied.

In the formation of the operculum from the central basal cells of the hymenium the first peridial initial divides and forms an intercalary cell

below in *C. pyriforme* (Adams, 1919), and if additional peridial initials arise from the same basal cell, each also forms an intercalary cell below, as in *C. comptoniae* (Adams, 1919), in this regard imitating the behavior of the spore initials which follow from the same basal cells (Fig. 78). It is possible that some of the later peridial cells do not have an intercalary cell, but of this insufficient observations have been made. When the lateral walls of the peridium are but one cell thick, *e.g.*, *C. comptoniae* and *C. pyriforme*, each peridial cell forms an intercalary cell from the outer lower surface, but when the lateral walls are two or more cells thick, as in *C. ribicola*, only the cells of the outer layer form intercalary cells (Fig. 79) except in rare instances (Kursanov, 1915, 1922).

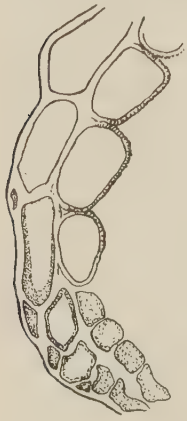


Fig. 79. — Lateral peridial wall of the aecium of *Cronartium ribicola*, two cells thick: intercalary cells occur in the outer layer only. (After Kursanov, 1915–22.)

In the third sub-group not much detailed information in regard to the development of the aecium in the several genera is yet available. It appears to follow in general the usual procedure seen in cupulate aecia, with the notable exception that the intercalary cells of the lateral walls of the peridium are cut off chiefly from the outer portion of the initial (Fig. 80), thus making them wedge-shaped. The peridium is one cell thick throughout. In Melampsora the peridium is rudimentary (Fig. 81), and has only been seen in *M. larici-populina* on *Larix decidua* (Hersperger, 1928). Although genera of the Melampsoraceae all have aecia to be classed as operculate, yet the walls of the peridial cells, when differing in thickness, are thicker on the inside than on the outside, in this respect being like those of cornute aecia and the reverse of cupulate aecia.

Fig. 80. — Chain of cells in a lateral peridial wall of *Uredinopsis mirabilis* on *Abies balsamea:* the intercalary cells are cut off from the lower outer edge of the spore initial, and soon deteriorate and become detached. (After Adams, 1919.)

The surface markings of the mature aeciospores in operculate aecia are especially characteristic. The wall of the spore consists of two layers, in many species the outer one being strongly verrucose over part or all of its surface (Fig. 82). The formation of warts or tubercles on

such spores is ascribed by Colley (1918) to early hardening of the outer layer and continued growth within, thus producing a tessellated cracking of the outer surface and the final verrucose structure.

(4) *Naked or caeomoid aecia.* — Probably more attention has been attracted to the development of the naked or caeomoid aecium than to any other kind of sorus. This is due in part to its simple structure, but more because of the interest attached to the study of cell fusions in this kind of sorus, ever since their discovery in Phragmidium by Blackman in 1904. Such aecia have been examined in detail by Sappin-Trouffy (1896), Blackman (1904), Christman (1905a), Blackman & Fraser (1906), Kursanov (1910, 1915, 1922), and Fromme (1912).

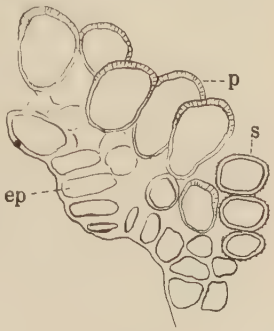


Fig. 81. — Part of young aecial sorus of *Melampsora laraci-populina* on *Larix decidua: p* peridial cells, *s* three aeciospores, *ep* epidermal cells. (After Hersperger, 1928.)

The aecia of this form are called naked, as they are not bounded by a peridium and rarely by paraphyses. The primordium is composed of hyphae which accumulate at a point immediately beneath the epidermis and continue to extend centrifugally. Within this primordium is developed a loose palisade of vertical hyphae with their tips against the epidermis. The apical cells lose their contents and become disorganized forming the so-called buffer cells (Fig. 83), which are the equivalent

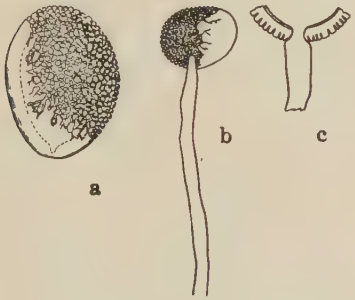


Fig. 82. — Aeciospores of *Cronartium ribicola: a* mature spore, the reticulated area extending over most of the spore; *b* a germinating spore; *c* section of the spore-wall and germ-tube. (After Colley, 1918.)

Fig. 83. — A young sorus of the caeomoid aecium of *Melampsoro lini: a* spore initials which have already cut off two sterile buffer cells *b* above. The buffer (plectenchyma) cells follow the contour of the epidermal cells above them. (After Fromme, 1912.)

of the plectenchyma in the more complex types of aecia (Fromme, 1914). The depth of the plectenchyma varies among different species, there being commonly only a single layer of buffer cells as in *Earlea speciosa* (Christman, 1905a). There is a double layer in *Melampsora lini* (Fromme, 1912), and a layer three to five cells deep in *M. rostrupii* (Kursanov, 1915, 1922).

The cells below the buffer layers enlarge somewhat, develop a denser protoplasm with larger nuclei, and give rise to the hymenium of basal cells by fusing in pairs. The basal cells proceed to cut off a succession of aeciospore initials, which are transformed into chains of aeciospores and intercalary cells, as described for other forms of aecia. Sporulation begins at the center of the hymenium and proceeds in centrifugal order toward the margins, which are not definitely delimited by layers of hyphae as in cupulate and cornute aecia. The extension of the hymenium may continue for some time after sporulation has begun at the center.

(5) *Stylosporic or uredinoid aecia.* — That the sorus commonly called a "primary uredo" is morphologically an aecium was first pointed out by Christman in 1907a. Sappin-Trouffy (1896) had previously suggested the homology between the pedicel of the stalked spore and the intercalary cell of aeciospores that are catenulately produced. The uredinoid aecium closely resembles the naked or caeomoid form in its development. The primordium is scant and arises just beneath the epidermis (Fig. 84). A single layer of buffer cells is produced in *Frommea obtusa* (Christman, 1907a), *Triphragmium ulmariae* (Olive, 1908b) and *Trachyspora alchemillae* (Kursanov, 1915, 1922). In *Puccinia suaveolens* they quickly disappear, and are scarcely to be recognized (Kursanov, 1915, 1922). The basal cells originate as in caeomoid aecia, and the indeterminate centrifugal extension of the hymenium is similar.

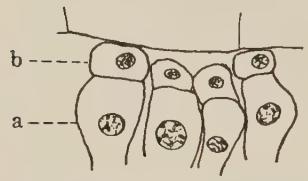


FIG. 84. — A young sorus of the stylosporic aecium of *Frommea obtusa* on *Potentilla canadensis: a* spore initials which have cut off a single layer of buffer cells *b* above. (After Christman, 1907a.)

The first aeciospore initial is produced from the basal cell as in the preceding forms. There is a marked difference shown, however, when the initial divides. The upper cell is changed into an aeciospore (also called a "primary uredospore") with an echinulate surface, instead of a verrucose surface as in nearly all other forms of aecia, and the lower cell elongates to form a pedicel from which the spore does not separate for some time.

In the meantime the basal cell prepares to cut off a second initial (Fig. 85), but instead of producing it directly beneath the now metamorphosed first initial and thus starting a chain of spores, as in other forms of aecia, it is produced as a bud at one side. In this way aeciospore formation is repeated a number of times, only one independent spore with its pedicel being formed each time from the successive lateral budding of the basal cell.

Fig. 85. — Young aeciospore with its pedicel from *Frommea obtusa*, and the beginning of a second spore at one side. (After Christman, 1907a.)

The development of uredinoid aecia in such genera as Ravenelia, Pileolaria, Uropyxis, Prospodium, etc., has not been studied, and details of the formation of these sori are unknown. It is reasonable to expect, however, that they conform in the main to the account given above.

(6) *Hyphoid aecia.* — A most remarkable form of aecium occurs in the genus Dasyspora, in which only one species is known, *D. foveolata* (Fig. 18). It may be designated the hyphoid or superficial aecium, as the sorus protrudes through a stoma and expands above the epidermis as a much branched colorless mass of hyphae (Fig. 86). The diameter of the hyphae is nearly as great as that of the aeciospores, and each septate branch is terminated by a colorless, verrucose spore, having a small, narrow, stalk cell, giving the appearance of a neck cell. Too little is known to warrant a statement regarding homologies.

Fig. 86. — Branched sporophores bearing aeciospores of *Dasyspora foveolata;* the spores drop away upon maturity. (Original.)

Uredinia and urediniospores. — Uredinia are of the nature of secondary or conidial sori, being derived from binucleate mycelium and giving rise through their spores to like binucleate mycelium. Being of a secondary nature, and in every case following aecia, they usually partake of the same general formation as do the aecia. Sometimes they closely resemble the aecia that precede them in the cycle, but more often they are quite dissimilar, yet in no case do they introduce a distinctly novel structure not to be found in some one of the several forms of aecia.

The uredinial sorus begins with a primordium, all the cells of which are necessarily binucleate as they arise from a mycelium of binucleate cells. As there is no fusion of cells at the base of the uredinium, the

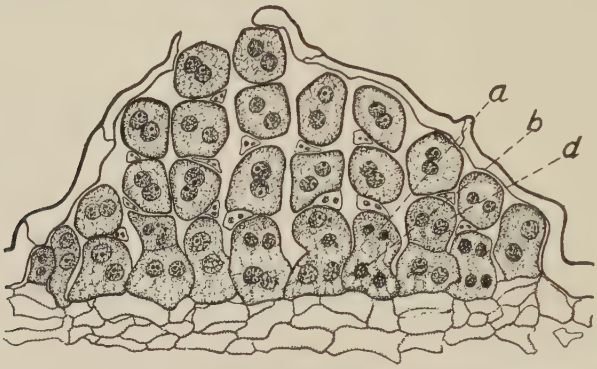


Fig. 87. — Section of young uredinial sorus of *Coleosporium solidaginis: b* basal cell, giving rise by slight lateral budding at *a* to form the spore initial *d*. Intercalary cells are small and formed at one side, while there is an entire absence of peridial cells. (After Moss, 1929.)

hymenial layer with its basal cells is usually not so distinct or rich in protoplasm as in the aecium. The general course of development resulting from the basal cells is about the same as a rule as in the aecium,

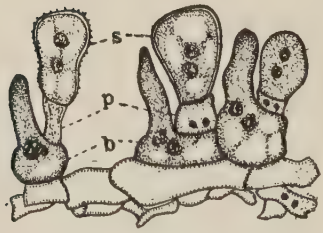


Fig. 88. — Development of pedicellate urediniospores of *Pucciniastrum myrtilli: p* pedicels bearing single spores; *b* basal cells, each budding to form a second spore. (After Moss, 1926.)

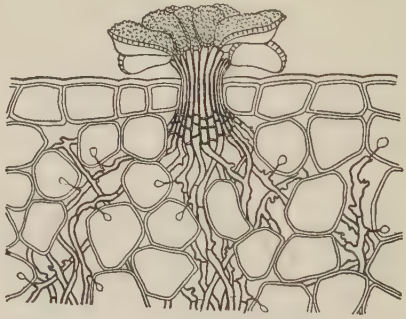


Fig. 89. — Sorus of *Hemileia vastatrix*, showing protrusion of the pedicels through a stoma, enabling the urediniospores to be borne above the surface of the host. (After Sydow, 1902–04.)

but usually more simplified. Whether the spores are catenulate (Fig. 87) or pedicellate (Fig. 88) their development follows the same methods respectively as described for the corresponding aeciospores (pp. 130, 140),

except that in Coleosporium the basal cell shows a tendency to imitate the pedicellate forms by budding (Moss, 1929). In certain genera, *e.g.*, Desmella and Hemileia, the sori arise immediately beneath stomata and push outward to form the urediniospores above the surface of the host (Fig. 89), thus giving the appearance of a superficial growth.

In cupulate uredinia, such as those in *Puccinia ambigua* on Galium, the close resemblance to the aecia that precede them obviates the need of further description, except that of course no cell fusions initiate the chains of spores.

In a somewhat similar way, but not to the same degree, the uredinia that follow stylosporic aecia are similar to the aecia that precede them in the cycle, but usually smaller and more circumscribed. In *Triphragmium ulmariae* (Kursanov, 1915, 1922) the resemblance is very close, even to the formation of a single layer of buffer cells above the hymenium, but differs in the abundant production of peripheral paraphyses, and in a more definite and usually smaller hymenium. When uredinia of the common form follow cupulate aecia, the development of the uredinia may be similar to the preceding, as in *Puccinia iridis* (Kursanov, 1915, 1922), even to poorly developed buffer cells, but more usually no buffer cells are formed, *e.g.*, *Puccinia allii* and *P. helianthi* (Kursanov, 1915, 1922). Peripheral paraphyses may or may not be present. Although there is usually a highly dissimilar structure in the uredinium as a whole, yet the urediniospores in some cases may imitate the aeciospores in shape and coloration, *e.g.*, in *Puccinia fraxinata* (Fig. 90 *a*) with aecia on ash trees (*Fraxinus* spp.) and the uredinia on marsh grass (*Spartina* spp.), in *P. seymouriana* (Fig. 90 *b*) with uredinia on same hosts as the

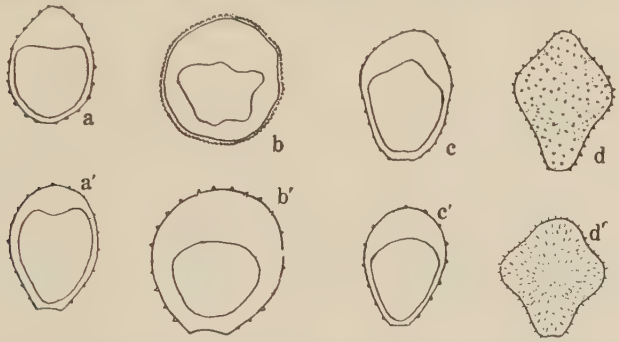


Fig. 90. — Similarity in form between aeciospores (upper) and urediniospores (lower) of same species: *a Puccinia fraxinata, b P. seymouriana, c P. verbenicola, d Olivea capituliformis.* (Original.)

last, but aecia on Cephalanthus and other hosts (Arthur, 1902b) and also in *P. verbenicola* (Fig. 90 *c*) with aecia on *Verbena* spp. and the uredinia on the grass, *Sporobolus* spp. (Arthur, 1900b). The urediniospores in these cases resemble the aeciospores in being obovate, and in having colorless walls that are greatly thickened above, while each retains its characteristic surface markings. In the very highly dissimilar sori in *Olivea capituliformis*, the aecia being sunken unusually deep in the leaf tissues and without peridia, while the uredinia are protruded through a stoma and expanded superficially above the epidermis with a circle of large and strongly incurved paraphyses, the urediniospores not only resemble the aeciospores (Fig. 90 *d*) in their brown color and in their remarkable stellate form, but also in surface markings, both being echinulate, which is a unique character for aeciospores except those of stylosporic forms.

Fig. 91. — Paraphyses surrounding the uredinium of *Prospodium bahamense:* the bases are united where they emerge from a stoma. Only one urediniospore drawn. (Original.)

Fig. 92. — Uredinium of *Phakopsora vignae* on Teramnus: the numerous paraphyses form a pseudoperidium by the union of their bases. (Original.)

Although paraphyses occur as inconstant factors in some species, in others when present they are usually in indefinitely large numbers, with more or less thickened walls, and markedly incurved. In some species they have their bases united. Sometimes, especially when the sorus arises beneath a stoma, a single ring of paraphyses are united into a contracted pedicel-like base, as in the West Indian rusts *Prospodium plagiopus* and *P. bahamense* (Fig. 91). More frequently the bases of the paraphyses form a pseudoperidium with extensions into the cavity of the sorus as in the tropical rusts *Phakopsora vignae* (Fig. 92), *P. aeschynomenis* and *Crossopsora notata*, in which the appearance is that of a cellular peridium having each cell prolonged on its inner side

into a highly developed paraphysis. Occasionally a single peripheral circle of paraphyses arises from a short peridial base of one cell thickness, as in *Aplopsora nyssae.*

FIG. 93. — Section of young uredinium of *Melampsora lini: a* initial of a peridial cell and its basal cell below, *b* peridial cells, *c* intercalary cell, *d* basal cell, *e* pedicel of spore, *f* urediniospore. (After Moss, 1929.)

In the somewhat anomalous genus *Melampsora* the urediniospores, which in some species are echinulate and in others verrucose, are borne singly on pedicels with capitate paraphyses intermixed (Fig. 8 B), these usually being slenderer when near the periphery, and in the immature sorus arch over the spores (Moss, 1928). There is formed, in addition, a rudimentary cellular peridium (Klebahn, 1899; Kursanov, 1915, 1922; Moss, 1929), derived from lateral initials in a manner resembling the procedure in cupulate aecia (Fig. 93). This poorly developed peridium largely disappears as the sorus matures, and naturally is not mentioned in systematic treatises. In *Melampsora lini* (Fig. 94) the paraphyses are metamorphosed spore initials (Fromme, 1912).

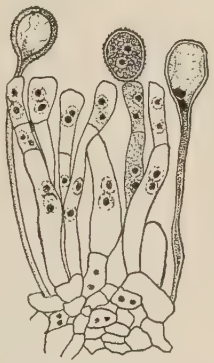


FIG. 94. — Part of uredinium of mature *Melampsora lini:* pedicels and elongated basal cells of the urediniospores with conjugate nuclei, only one pedicel with spore remaining attached; two capitate paraphyses. (After Fromme, 1912.)

The genera Hyalopsora, Uredinopsis and Milesia, which are fern rusts, together with the genus Melampsorella (Fig. 95), develop a peridium about the uredinium, which is composed of much elongated cells at the sides, sometimes reinforced by similar yet shorter cells outside, the inner cells joining above with isodiametric cells to form a dome. This peridium, which is delicate and consists of cells with unthickened walls, is usually difficult to see when mature, especially in dried material. In the genera Pucciniastrum, Melampsoridium and

Cronartium a uredinial peridium one cell thick, consisting of isodiametric cells both at the sides and above, is otherwise very similar to that in the four genera previously mentioned, but more firm and with a pronounced differentiation of apical cells to form a central ostiole (Figs. 20 and 21). In species of Pucciniastrum the evolution of the ostiole

Fig. 95. — A young uredinium of *Melampsorella elatina* on Abies. (After Moss, 1926.)

has been described and figured by Dodge (1923b). In Melampsoridium, however, the ostiolar cells are most characteristic, each cell being prolonged into a sharp point (Fig. 96). The development of the sorus in these genera, which has been studied more or less fully by Bartholomew, Colley, Dodge, Kursanov, Ludwig & Rees, and Moss, shows no marked difference from that of other sori with similar structures, the peridial cells being either metamorphosed spore initials or metamorphosed spores.

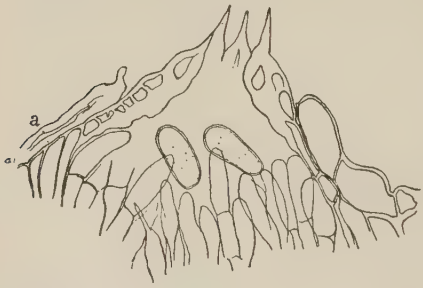


Fig. 96. — Uredinium of *Melampsoridium betulinum*, especially showing the pointed ostiolar cells and the reinforcing cells *a* at the sides. (After Fischer, 1904.)

In the three fern genera, Hyalopsora, Uredinopsis and Milesia, the urediniospores are noticeably dimorphic. This dimorphism in the case of *Hyalopsora polypodii* was found by Dietel (1911b) to be correlated with the succession of the sori, the spores first formed having thin walls and the later ones thick walls (Fig. 97). In a study by Moss (1926) the thick-walled spores are shown to be of the same nature as the amphispores of grass and sedge rusts (p. 16).

The urediniospores of Hyalopsora and other genera of the Pucciniastreae are variously described as sessile, pedicelled, or catenulate, and

the studies especially directed to this question by Ludwig & Rees (1918), Dodge (1923b), Lindfors (1924) and Bell (1924) did not reach full agreement. The detailed studies by Moss (1926) on Uredinopsis, Hyalopsora, Milesia, Pucciniastrum, and Melampsorella, show that these genera, which with Melampsoridium belong to the family Pucciniastreae, possess pedicellate urediniospores, arising by lateral budding (Fig. 88). The pedicels are often very short and difficult to demonstrate.

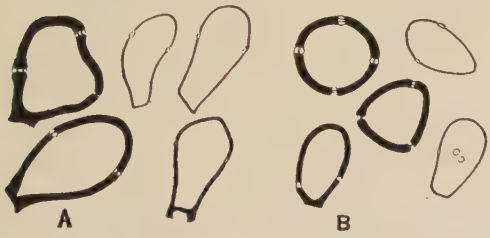


FIG. 97. — Urediniospores of Hyalopsora with thick and thin walls: *A* from *H. aspidiotus*, *B* from *H. polypodii*. (After Moss, 1926.)

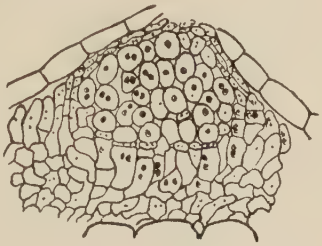


FIG. 98. — Uredinium of *Melampsoropsis pyrolae*, showing catenulate spores with intercalary cells, and a peridium two cells thick. (After Kursanov, 1915–22.)

In Coleosporium and Melampsoropsis (Chrysomyxa) the urediniospores have colorless and verrucose walls, and are catenulate with intercalary cells. Their development presents, so far as known, no marked deviation from other sori with catenulate spores. An evanescent peridium in *Melampsoropsis pyrolae*, two cells thick (Fig. 98), has been considered by Kursanov (1915, 1922) as anomalous. In Coleosporium no peridium is known (Moss, 1929).

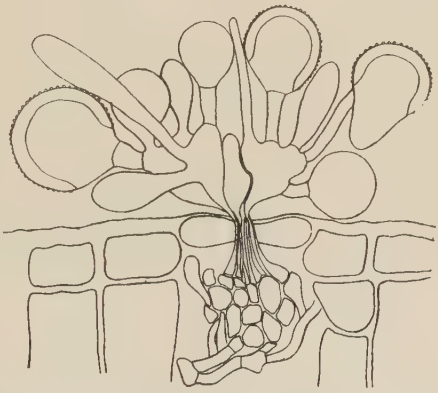


FIG. 99. — Telium of *Cystopsora oleae:* the basal cells push through the stoma and enlarge above the surface of the host; spore initials form as lateral buds giving rise to pedicellate teliospores. (After Butler, Ann. Myc. **8** : pl. 6.)

TELIA. — The telial sorus, like that of the uredinium, introduces no marked features not already described for the aecial sorus. In a few instances, *e.g.*, Cystopsora, the sorus pushes through a stoma and by forming the teliospores above the surface of the host gives the appearance of being superficial (Fig. 99). In one

known species of rust, native of Java, *Goplana mirabilis*, a portion of the mycelium becomes superficial, and on this part the telia are borne (Fig. 100). The rust is microcyclic with colorless spores (Raciborski, 1909).

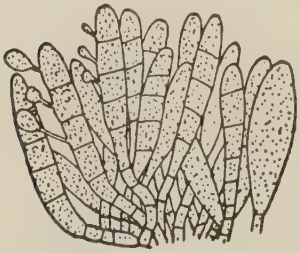


FIG. 100. — Telium of *Goplana mirabilis*, with part of the spores germinating. A large paraphysate cell at right. (After Sydow, 1912–15.)

Teliospores produced singly, either pedicelled or sessile, are the most common form, and these may consist of one or more cells, while catenulate teliospores also occur, but are less common.

The pedicellate teliospores arise singly from lateral buds of the basal cells (Fig. 101) in the manner customary for stylosporic aecia and the ordinary uredinia (pp. 140, 141). The subsequent division into two (Fig. 102) or more cells, the dominant number being characteristic of different genera, is brought about by the successive division of the young teliospore. The uppermost cell in the series is usually the oldest. Catenulate teliospores are produced by successive

FIG. 101. — Teliospores of *Puccinia podophylli* arising from a basal cell by successive lateral budding. (After Christman, 1907b.)

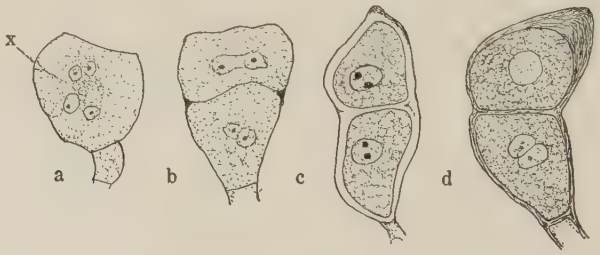


FIG. 102. — Formation of two cells in a teliospore of *Puccinia glumarum: a* young teliospore and pedicel, after the conjugate nuclei have divided to form two pairs, and the septum has begun to form at *x*; *b* fusion of the conjugate nuclei is in progress and the septum placed; *c* spore nearly mature, the fusion nucleus still retains the two nucleoli; *d* mature teliospore with delayed nuclear fusion in one cell. (After Allen, 1928.)

divisions of the basal cell, in the same manner that catenulate aeciospores and urediniospores are formed (pp. 130, 142).

In *Cronartium ribicola*, having pedicellate urediniospores and catenu-

late teliospores forming long columns, both inclosed by a cellular peridium in the early stages, "it is impossible to tell very young uredinia and telia apart" (Colley, 1918). It may be safely assumed that the primordium of most macrocyclic telia has the same form as the uredinium preceding it in the same species. As the uredinium is usually without space-making cells above the hymenium, so in the telium such cells above the hymenium are usually absent, or else reduced to one or two layers of so-called buffer cells. In Gymnosporangium, a genus without uredinia, it has been shown that in subepidermal telia, *G. juniperi-virginianae*, *G. globosum*, *G. clavariaeforme* and *G. nidus-avis* (Dodge, 1918b), as well as in subcuticular telia, *G. germinale* (Dodge, 1922), the first cells produced are buffer cells. In some species these are unusually long (Fig. 103). The basal cells then bud off a succession of laterally formed teliospores in the manner already described for pedicellate aeciospores (p. 141). The microteliospores of *Puccinia xanthii* also form buffer cells (Walker, 1927), but the correlated macrocyclic *P. canaliculata* on Cyperus has not been studied for this feature.

FIG. 103. — Buffer cells of unusual length in the telium of *Gymnosporangium fraternum* on Chamaecyparis. (After Dodge, 1918a.)

FIG. 104. — Young spore of *Polythelis fusca* showing the subpedicellate cell, that unites with others to form a common stalk for a group of spores. (After Walker, 1927.)

The development of the telial primordium in such genera as Coleosporium, Melampsora, Melampsoropsis, Melampsorella, Uredinopsis, Milesia, Hyalopsora, Pucciniastrum, in which the teliospores are sessile and arise under the cuticle, or within or beneath the epidermis, has received little study. This is also true of the similar, but somewhat catenulate teliospores of Phakopsora and Cerotelium, as well as of some genera with pedicellate spores, such as Cystopsora, Uropyxis, Ravenelia, etc. In the last-named genus the teliospores form capitulate groups surrounded by adnate, colorless cysts (Figs. 25 *s* and 43 *B*). In the genus Tranzschelia and the correlated microcyclic genus, Polythelis, the pedicels undergo a second division (Fig. 104) to form two cells (Walker, 1927). The lower

cells of the pedicels adhere in groups to form a persistant basal stalk characteristic of this genus.

Telia are generally without paraphyses or peridia, although these elements occur in a limited number of species. In some species with subepidermal telia, as *Puccinia allii*, *P. gladioli* (Fig. 8 *c*), *P. coronata* (Fig. 105), *P. rubigo-vera*, and *P. glumarum*, the uredinial paraphyses, usually inconspicuous and scantily produced, are represented in the telia by much modified and compacted subepidermal paraphyses. In such cases each element is a metamorphosed initial which remains undivided, as shown by Kursanov (1915, 1922) for *P. allii*, a liliaceous species. The telium of this last species is compound, as is also often the case with grass rusts (Fig. 105), being composed of groups of teliospores, each group surrounded by subepidermal paraphyses. Both the teliospores and paraphyses are produced from basal cells which are at first indistinguishable. In their formation the initials around the circumference of each hymenial group soon show a clearer and more watery protoplasm. Each of these peripheral initials elongates, but without dividing, and the wall thickens and turns brown. At first some protoplasm with two nuclei can be seen, then the contents of the cell soon disappear, resulting in the characteristic subepidermal paraphysis.

Fig. 105. — Section parallel to surface of host through a compound telium of *Puccinia coronata* on *Avena sativa*, showing the subepidermal paraphyses surrounding the groups of spores. (After Bolley, 1889b.)

Microtelia and their spores. — As the search for gold by the alchemists led to discoveries in chemistry, so the search for organs of fertilization brought to light a great fund of information regarding the comparative structure and development of the rusts, and in no group more than in the short-cycle or microcyclic forms. This knowledge is here summarized as briefly as possible.

The study of microcyclic rusts is especially interesting in view of

the evident genetic relation existing between them and macrocyclic species with similar structural features and host relationships. The microcyclic rusts may be placed in four categories, corresponding to various degrees in which they simulate the aecia of corresponding macrocyclic species: (1) close resemblance in development of the sorus and spores, as well as in gross appearance, *e.g.*, species of Endophyllum; (2) resemblance in development and gross appearance, but not in spores, the sorus being deep-seated, *e.g.*, *Puccinia grindeliae;* (3) resemblance in development, but not in gross appearance or form of spores, the sorus being deep-seated, *e.g.*, *P. asteris;* (4) resemblance in development, but not in spores, the sorus being shallow, *e.g.*, *P. epilobii.*

For the first category, in which both sorus and spores are like those of aecia in certain macrocyclic species, *Endophyllum sempervivi* on Echeveria and Sempervivum is an excellent example (Fig. 106). It is much like the aecia of certain grass rusts in both sorus and spores, *e.g.*, in *Puccinia australis*, but the germination is that of a typical teliospore (Fig. 28 *B*). Similarly and even more definitely, *Endophyllum tuberculatum* on various genera of the Malvaceae is the counterpart of the aecia of the Stipa rust, *Puccinia interveniens. Kunkelia nitens* is caeomoid, and only to be told with certainty from the aecia of its long-cycle form, *Gymnoconia interstitialis*, by the spore germination. The development both of Endophyllum and Kunkelia have been studied in detail, and shows close likeness to that of corresponding aecia up to the time of the protrusion of a germ-tube from the spores.

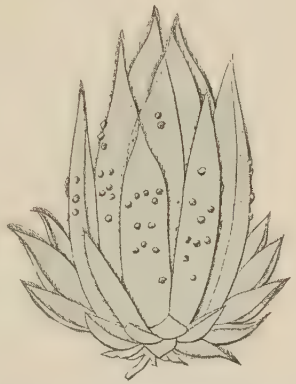


Fig. 106. — *Endophyllum sempervivi* on *Sempervivum hirtum.* (After Kerner, Pflanzenleben.)

In the second category may be placed *Puccinia grindeliae*, a short-cycle species, which is found on similar and partly the same composites as the aecia of the long-cycle grass rust, *P. stipae.* It bears close resemblance in the form of its spores to the teliospores of *P. stipae*, but the sorus both in its form and its reaction to the host is otherwise a close imitation of the aecial sorus of that species and not of its telial sorus. The characteristic effect of the fungus on the host in reinforcing the sorus and only permitting dehiscence by a central pore is the same for the microcyclic species as for the aecia of the corresponding macrocyclic species. Moreover, one often finds in the sori of the microcyclic species, especially

when they are accompanied by pycnia, as occurs on some hosts and not on others, a few free aeciospores and peridial cells, which have the characters of those in the aecia of the correlated macrocyclic species. While no study of the development has been made, yet it may reasonably be assumed that these loose aeciospores and peridial cells, always found in the upper part of the mature sorus, have been derived from the first few initials cut off by some of the basal cells. In *Puccinia grindeliae* the sorus doubtless starts out in the form of an aecium with a transitory production of aeciospores and peridial cells, simulating those of *P. stipae*, but finishes with the production of spores like the teliospores of that species. Possibly the evolution of *P. grindeliae* has been brought about by the telescoping of the drawn-out cycle of *P. stipae*.

Fig. 107. — Primordium of *Uromyces scutellatus*, showing binucleate cells in the plectenchyma, which will become disorganized along with the uninucleate cells. (After Kursanov, 1915–22.)

The microcyclic species, *Uromyces scutellatus* and *U. levis*, both on species of Euphorbia, are in the same category with *Puccinia grindeliae*. Both of the corresponding macrocyclic species have aecia on Euphorbia with uredinia and telia on leguminous hosts. They have been studied in detail (Kursanov, 1915, 1922), and their early development is shown to be fashioned after that of cupulate aecia. The vegetative mycelium, which is diffused and uninucleate, forms a rounded primordium. The formation of plectenchyma is delayed and the binucleate cells which appear at the base of the primordium form short filaments of binucleate cells which grow up into the plexus above. As formation of the plectenchyma proceeds the upper cells of the binucleate hyphae become disorganized along with the uninucleate cells in the same region (Fig. 107). The apical cells of lower unchanged parts of the binucleate hyphae then function as basal cells and bud off the spores. Such formation of a hymenium is similar to that described for some types of aecia (p. 133). The sori of the two species under discussion further simulate aecia in the production of a few peridial cells and aeciospores. There is no organized peridium, the peridial cells being isolated and

intermixed with the spores. They are of normal structure and are usually seen near the periphery. The aeciospores may occur singly or in short chains with intercalary cells. It appears evident that these sori begin like aecia but mature like telia.

As an illustration of the third and much largest category, in which the microcyclic rust resembles both in sorus and spores the telia of a macrocyclic rust, may be mentioned *Puccinia asteris*, occurring on various species of Aster and related genera. The corresponding macrocyclic rust is *P. asterum* (*P. extensicola*), which has cupulate aecia on the same or similar species of hosts affected by the microcyclic rust, and its uredinia and telia on various species of *Carex*. The primordia of this type are deep-seated, with an abundance of plectenchyma. The sori form more or less concentric and compacted groups, with some hypertrophy of the host, which is also true of the aecia of the corresponding macrocyclic species. Other microcyclic species of this type that have been studied are *Puccinia rossiana*, *P. asarina*, *P. fergussoni*, and *Uromyces ficariae* (Kursanov, 1915, 1922). The last species also develops a few urediniospores in the microcyclic sorus.

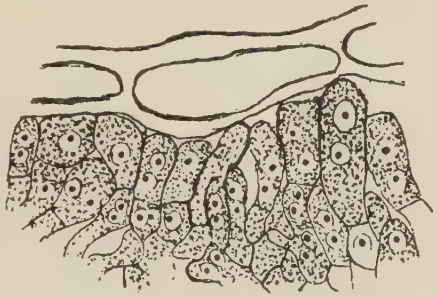


Fig. 108. — Primordium of *Puccinia conferta* on Artemisia: the binucleate fertile cells reach to the epidermis, and no sterile cells are present. (After Kursanov, 1915–22.)

As an illustration of the fourth category may be mentioned *Puccinia epilobii*, which has been studied by Lindfors (1924). The primordia of the sori of this type are typically shallow layers beneath the host epidermis with no resemblance to cupulate aecia. Examples of this type whose development has been studied in detail are *Uromyces gageae*, *Puccinia aegopodii*, and *P. conferta* (Fig. 108), the last being on Artemisia, reported as *Artemisia* sp. (Kursanov, 1915, 1922). Other species that have not been studied cytologically are *Puccinia adoxae* and *P. ligustici*, the first correlated with the macrocyclic species *P. nolitangeris* and the last with *P. polygoni-vivipari*. The sori are usually widely scattered, with little or no hypertrophy of the host, and in this particular resemble the aecia of the corresponding macrocyclic species.

Species of microcyclic rusts belonging to the Pucciniaceae which have been studied, in addition to those mentioned above, are *Puccinia lilia-*

cearum on Ornithogalum (Sappin-Trouffy, 1896; Maire, 1899), *P. buxi* on Buxus (Moreau, 1914), *P. malvacearum* on Malva (Werth & Ludwigs, 1912), *P. transformans* on Tecoma (Olive, 1908a), and *Polythelis fusca* on Anemone (Pavolini, 1912; Lindfors, 1924).

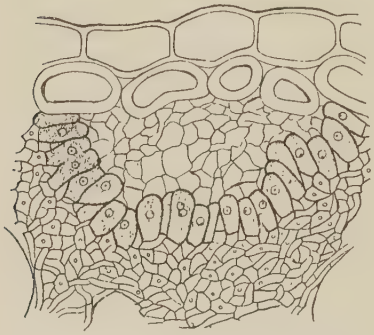


Fig. 109. — Primordium of *Chrysomyxa abietis:* the hymenial layer, beginning to show cell-fusions, separates the uninucleate basal hyphae from the plectenchyma above. (After Lindfors, 1924.)

Two microcyclic rusts belonging to the Melampsoraceae have been studied in considerable detail. One is *Chrysomyxa abietis* on Picea, corresponding in the general structure of its sori to the telia of macrocyclic species of Melampsoropsis having their aecia on Picea and their uredinia and telia on ericaceous hosts. In *C. abietis* an ample primordium (Fig. 109) is formed (Kursanov, 1915, 1922), which soon differentiates into a plectenchyma above of gradually disintegrating cells and a denser fertile part below. Fusion of cells takes place rather sparingly, so that the fertile basal cells do not touch each other to form a compact hymenium. Each active basal cell cuts off an initial which enlarges and often divides, becoming a rounded usually thick-walled spore-like body. The spore-like body may become divided into other cells by the formation of cross or longitudinal septa, each one of which produces a branching filament of thin-walled cells constituting the teliospores (Fig. 110).

Fig. 110. — Branching chains of teliospores of *Chrysomyxa abietis.* (After Kursanov, 1915–22.)

In *Gallowaya pinicola,* a microcyclic rust on *Pinus virginiana,* the primordium (Fig. 111) consists of uninucleate cells which grow chiefly towards the epidermis and eventually rupture it (Dodge, 1925). Fusions occur between the third or fourth cells from the upper ends of these hyphae and the binucleate cells that result cut off the spores in catenulate order. The end or buffer cells of the hyphae which rupture the epidermis of the host form a rather persistent peridium.

In germination the basidia in Gallowaya are formed internally

(Fig. 112). Each basidium of four cells is supported on a short promycelial stalk (Fig. 112 *b*).

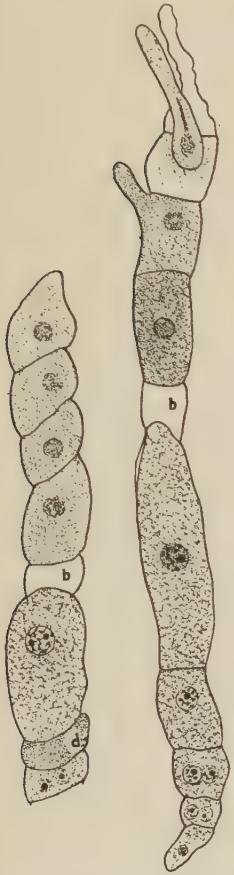


Fig. 112. — Two chains of germinating spores of *Gallowaya pinicola:* each terminal spore has formed an internal basidium of four cells, supported on a promycelial stalk *b*, and one spore has begun to form three sterigmata. (After Dodge, 1925.)

Prehymenial fusions. — There are some rusts in which the binucleate state appears prior to the formation of the hymenium. The species in which this is known to occur, in addition to the macrocyclic *P. caricis,* already mentioned (p. 130), are *Puccinia adoxae, Uromyces scillarum* (Blackman & Fraser, 1906), *P. fergussoni, P. asarina, P. conferta, U. gageae* (Kursanov, 1915, 1922), and *P. albulensis, P. arenariae, P. epilobii, P. gigantea, P. holboellii, P. saxifragae, U. solidaginis* (Lindfors, 1924), all belonging to the Pucciniaceae. The exact place and the method by which the first cell of the dikaryon is formed have not been determined for these species although they have been studied especially with these points in mind. In each of the species just mentioned microtelia only are produced, pycnia as well as other sori being absent. The primordium is formed of binucleate mycelium and the vegetative hyphae which precede the primordium are also binucleate. It has been suggested that a transition from uninucleate to binucleate cells occurs early in the growth of the mycelium from the basidiospore, but the existence of such a transition has not been demonstrated. It seems evident that cytologic studies, using controlled cultures, will be necessary for a thorough understanding of species of this sort.

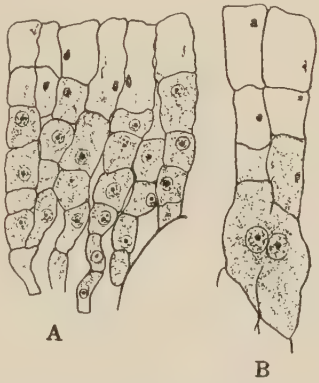


Fig. 111. — Part of the primordium of *Gallowaya pinicola: A* before cell-fusion has begun; *B* one fusion-cell has formed. Each row of cells terminates in one to three buffer cells. (After Dodge, 1925.)

In two microcyclic rusts, *Uromyces scutellatus* and *U. levis*, chains of binucleate cells not only arise in the lower part of the fertile area, as previously explained, but extend through and beyond the hymenium, so that the sporogenous layer is formed from intermediate cells of the chains, the upper cells, although binucleate, degenerating with the uninucleate cells of the plectenchyma (p. 152).

ABNORMAL DEVELOPMENT

Such deviations from normal behavior of the nuclei as are noted in the following paragraphs may be considered either as indicating a tendency toward a pathologic condition, or on the other hand may be regarded as the final product of a regressive evolution.

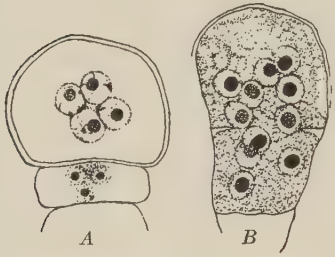


Fig. 113. — Multinucleated aeciospores in *Melampsoro lini: A* aeciospore with four nuclei and an intercalary cell with three; *B* spore initial with eleven nuclei, dividing to leave seven nuclei in the aeciospore. (After Fromme, 1912.)

Multiple nuclei. — Although two nuclei in each cell, forming a dikaryon, is usual and normal in the sporophytic stage of the rusts, the occurrence of more than two nuclei in both vegetative cells and spores has been frequently observed. The production of aeciospores with four nuclei or more (Fig. 113) is not uncommon in *Melampsora lini*, while trinucleate aeciospores (Fig. 114), have been traced to the fusion of three uninucleate basal cells (Fromme, 1912). In such cases the several nuclei divide simultaneously, forming separate spindle figures.

Fig. 114. — A chain of trinucleated aeciospores arising from the fusion of three uninucleate basal cells in *Melampsora lini*. (After Fromme, 1912.)

Kursanov (1915, 1922) found urediniospores in the sorus of *Puccinia suaveolens* with as many as eight nuclei, and cells of the mycelium with as many as five nuclei. Many additional examples of plurinucleate vegetative and reproductive cells in other species could be cited.

In a certain physiologic form of *Puccinia rubigo-vera tritici* infection experiments by Allen (1926b) using binucleate urediniospores usually gave four nuclei in the appressorium, eight in the substomatal vesicle, and a resulting mycelium with six nuclei at first, changing gradually to three nuclei, but with only one nucleus in the haustorium. Occasionally

fusion occurred between appressoria (Fig. 115 A), between substomatal vesicles (Fig. 115 B) and between hyphae in the vicinity of a forming uredinium (Fig. 115 C). The detailed nuclear behavior during fusion, or in the production of binucleate urediniospores from the trinucleate mycelium, has not been worked out.

In *Puccinia glumarum* the substomatal vesicles and the swollen hyphae that proceed from the vesicles are at first non-septate and multinucleate (Fig. 116). These nuclei are irregularly scattered, but when mycelial septation begins, after a period of about ten days, the nuclei arrange themselves in pairs and eventually the cells of the mycelium attain the usual binucleate condition. The haustoria with rare exceptions are uninucleate, even from multinucleate hyphae (Allen, 1928).

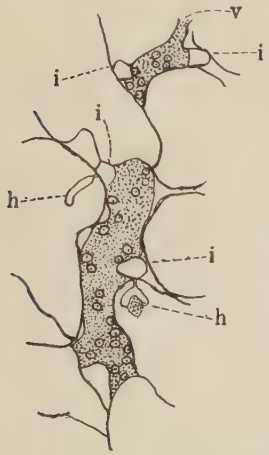


FIG. 116. — A multinucleate hypha in *Puccinia glumarum*, arising at *v* from a multinucleate substomatal vesicle. Hyphae at this stage of about six-days' growth are much swollen, conform closely to the intercellular spaces, and are without septa, except to cut off the haustorium initials; *i i i i* haustorium initials, *h h* haustoria, one of them clasping a cell nucleus. (After Allen, 1928.)

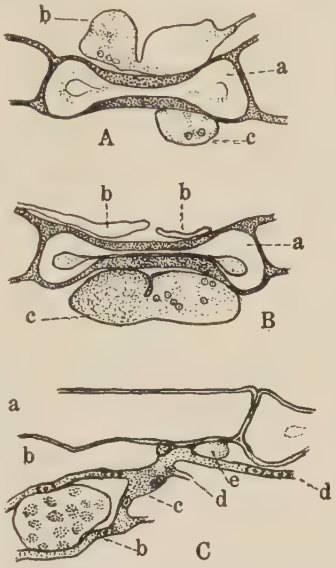


FIG. 115. — Fusion of hyphal cells in *Puccinia rubigo-vera tritici*: *A* between appressoria, *a* cell of stoma, *b* two fused appressoria, *c* the resulting substomatal vesicle; *B* between substomatal vesicles, *a* cell of stoma, *b b* two collapsed appressoria, *c* the resulting substomatal vesicles after fusion; *C* fusion between two intercellular hyphae, *a* epidermal cell, *b b* two hyphae before fusing at *c*, *d d* after fusion, one hypha having collapsed, *e* haustorium initial. (After Allen, 1926b.)

Extra nuclei in the basidiospores are met with at times. Basidiospores in *Coleosporium solidaginis* were found by Holden & Harper (1903) to possess two nuclei, and Poirault & Raciborski (1895) observed the same condition in *Coleosporium euphrasiae*, likewise Colley (1918) in *Cronartium ribicola*. Lindfors (1924) also found the same condition in a two-celled promycelial race of *Puccinia arenariae*. Dodge (1925) has detected a

similar binucleate condition in basidiospores of *Gallowaya pinicola*, but considers from their reaction to stains that only one of the nuceli is active. In other cases one of the nuclei apparently degenerates before germination of the basidiospore. In some cases germination begins with a precocious division of the nucleus, and the two resulting nuclei pass out of the basidiospore and then are separated by a division wall, thus producing a uninucleate mycelium. It does not necessarily follow, therefore, and even may never follow, that binucleate basidiospores give rise to a binucleate mycelium.

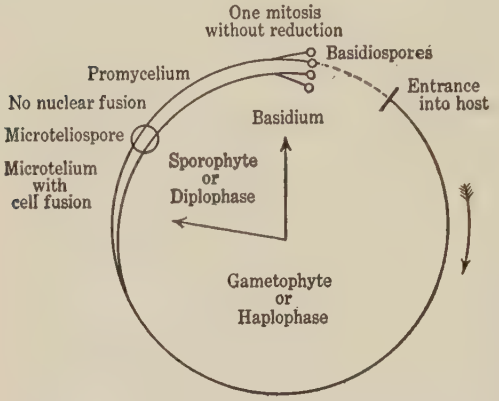


FIG. 117. — Diagram to show the nuclear course in a microcyclic rust with cell fusion but without nuclear fusion or reduction. (Original.)

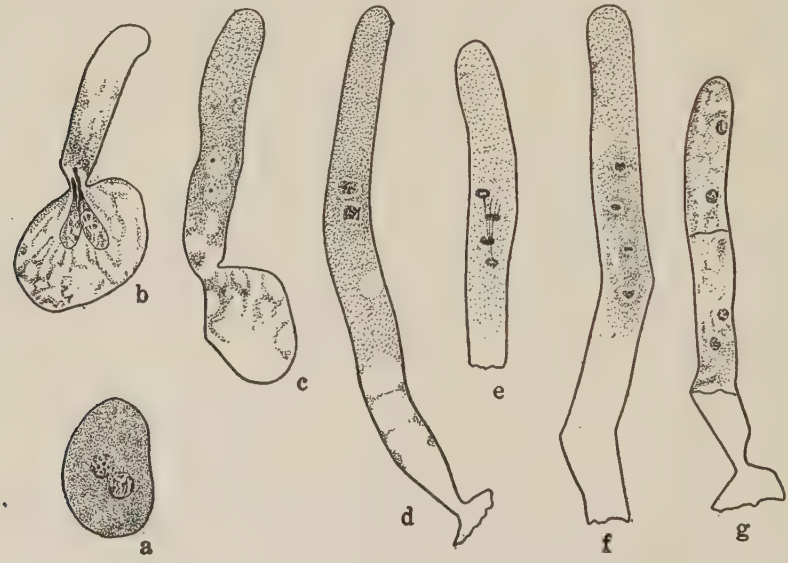


FIG. 118. — Nuclear behavior in a germinating spore of *Kunkelia nitens; a* mature spore, *b* nuclei migrating into germ-tube, one slightly in advance, *c* two nuclei in germ-tube, one beyond the other, *d*, *e*, *f* various stages in nuclear division, *g* the pairs of sister nuclei separated by the first cross-wall of the promycelium. (After Dodge & Gaiser, 1926.)

Binucleate races without nuclear fusion. — In some instances the dikaryon may change into the four nuclei of the basidium without undergoing the usual processes of fusion and reduction (Fig. 117). A carefully controlled study by Dodge and Gaiser (1926) of a race of the microcyclic rust on Rubus, *Kunkelia nitens*, has shown this condition. In this race when the two nuclei of the spore (Fig. 118 *a*) pass into the promycelium (Fig. 118 *b*) as a rule one of them somewhat precedes the other or subsequently slips past it (Fig. 118 *c*). Each of the nuclei of the dikaryon undergoes the usual mitosis (Fig. 118 *d–f*), but when the first wall of the basidium is laid down it leaves sister nuclei in each of the two cells (Fig. 118 *g*). Secondary walls are then formed, and uninucleate basidiospores result, which are to all appearances like those of other rusts. The same behavior is seen in *Endophyllum euphorbiae-sylvaticae* (Sappin-Trouffy, 1896; M. & Mme. Moreau, 1919), and doubtless occurs in other microcyclic species.

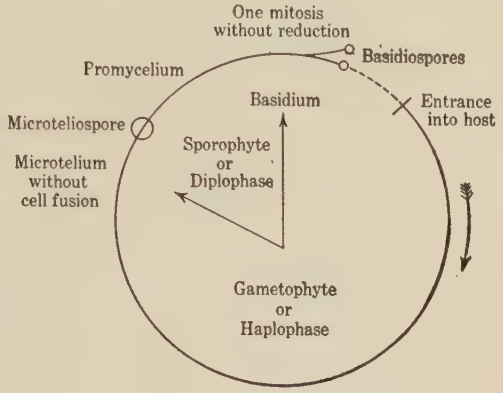


Fig. 119. — Diagram to show the nuclear course in a uninucleate microcyclic rust. (Original.)

Fig. 120. — Chains of aeciospores from *Ochropsora ariae* on Anemone: one chain binucleate, the other uninucleate, from the same sorus. (After Kursanov, 1915–22.)

The feature of especial interest in this connection is that although the sporophytic stage is concluded without nuclear fusion or chromosomal reduction yet all the other essential phases of a microcyclic alternation of generations has been accomplished.

Uninucleate races. — Races, in which the spores and all accessory cells of the sorus, as well as the vegetative hyphae, contain but single nuclei (Fig. 119), have been observed in *Uromyces rudbeckiae* (Olive, 1911b), *Endophyllum euphorbiae* (Moreau, 1912, 1915), *E. centranthi-rubri* (Poirault, 1913, 1915), *Tranzschelia punctata* and *Ochropsora ariae* (*O. sorbi*) (Kursanov, 1914, 1915, 1922), and *Kunkelia nitens* (Dodge, 1924c). In the last two

species the sorus may in some instances contain both uninucleate and binucleate spores in separate chains, the nuclear number corresponding to that of the basal cells from which the chains arise (Fig. 120). A uninucleate race of *Endophyllum euphorbiae*, discovered by Mme. Moreau (1912), and later named *E. uninucleatum*, has received prolonged study by the Moreaus (1919). Uninucleate races are often lacking in pycnia and the basidia may be only two-celled (Dodge & Gaiser, 1926).

CHAPTER V

DISSEMINATION AND GEOGRAPHIC DISTRIBUTION

Dissemination of spores: abundance; forcible discharge; movements due to gravitation, convection currents, wind, water, animals, human agency; alien species; restrictions to dissemination.

Geographic distribution: incomplete knowledge; names of unequal value; abundance of individuals; indigenous and endemic rusts; climatic zones; Uromyces and Puccinia; lengthening of the life-cycle; shortening of the life-cycle; microcyclic species; leptosporic species.

Barriers to distribution: oceans, mountains, deserts, climate; facility of germination; hosts; connected and isolated regions; sporadic occurrence of microcyclic species.

Distribution by groups of hosts: ferns, gymnosperms, monocots, dicots; groups without rusts.

Distribution in time: geologic record.

DISSEMINATION OF SPORES

The spores of rusts are formed in large numbers in sori on or immediately beneath the surface tissues of living plants. Each sorus as a rule contains many spores. The spores are either retained within the sorus, or they are liberated by various means and are readily dispersed through different agencies. Most teliospores and some amphispores remain in the sorus and germinate where formed, and in such cases all the spores of a sorus are about the same age and reach maturity at nearly the same time. But nearly all aeciospores and urediniospores together with pulverulent teliospores become detached from the sorus as they mature, and in such cases a succession of spores often continues through a considerable period of time.

Number of spores produced. — The number of aeciospores in an average aecium of *Puccinia eatoniae* has been determined by Fromme as 8,000 or more (1914, p. 25), and in the aecium of *Puccinia graminis* an average of 11,000 were found by Buller (1924, p. 550). Buller (1924) also made detailed calculations at Winnipeg, Canada, of the number of aeciospores likely to be formed on a barberry bush bearing some 200 leaves, all fairly well infected, and reaches the astonishing number of 1,000,000,000. Even this number is exceeded in a careful computation made four years later in Rice County, Minnesota, by Christensen (unpublished data), who found that a single barberry bush would bear 64,512,000,000 aeciospores. In most instances a succession of spores

will be produced, and consequently even these figures in some cases may be exceeded. However, as in other organisms having a high potential fecundity, many causes act to reduce the actually effective results.

The number of spores in the ordinary uredinium seems not to have been counted, but while it probably falls below that recorded for aecia, the greater number of uredinia on a host, and their more rapid and continued multiplication would doubtless make the total number of spores for a season equal or even much exceed that from aecia. The repeating nature of the uredinia of grass and similar rusts makes the liberation of urediniospores follow a geometric progression. Under epidemic conditions the spores of such species as *Puccinia graminis tritici* and *P. rubigo-vera tritici* are formed in such prodigious numbers that they may rise in a cloud around the harvester.

The number of basidiospores produced by a single gall ("cedar-apple") of *Gymnosporangium juniperi-virginianae* according to an estimate made by Lloyd and Ridgway (1911) may amount to 7,000,000,000. This estimate assumed that each of the two cells of the teliospores produced three germ-tubes, an assumption doubtless based on the misleading statements of Farlow (1880). But as only one efficient germ-tube is usually produced from a cell (p. 208), the figure is evidently three times too large. However, the galls of Gymnosporangium vary greatly in size, and it is quite likely that the original estimate may not be too great for some of the large galls.

Such astonishing reproductive powers are common for most plants from elm trees to puffballs and simpler forms, and even for many animals. But even when coupled with no less marvelous methods of dispersal only a small fraction of the reproductive agencies succeed in establishing new individuals.

Forcible discharge. — That the spores of various fungi belonging to the Ascomycetes and Basidiomycetes are forcibly projected from their original attachment has been known for more than a century, and in recent years the phenomenon has been subjected to careful experimental study. Only in the last few years have the same kind of movements been seen among the rusts. Zalewski (1883) was probably the first to record observations on the forcible discharge of aeciospores and Klebahn (1904a) on basidiospores, and within the last fifteen years many other persons have made careful studies.

Basidiospores in the genera *Uromyces*, *Puccinia*, *Cronartium*, *Coleosporium*, *Endophyllum*, *Gymnosporangium*, and doubtless in other genera,

according to various observers (Coons, 1912; Dietel, 1912b, 1915; Buller, 1922, 1924), are shot upward 0.2 to 0.3 mm., and horizontally 0.3 to 0.8 mm., according to size of the spores. Dietel (1912b) estimates the initial velocity to be 8 to 9 cm. per second. The basidiospores are assured a better distribution by the position of the basidium, which becomes curved (Fig. 29 *a*) so as to lie horizontal to the supporting surface, thus permitting the spores to be shot directly upward into the air.

Shortly before the basidiospore is discharged from the sterigma a drop of water is excreted at the hilum and is carried away with the spore (Fig. 121). Although the drop of water is closely associated with the maturing of the basidiospore, it is doubtful if it forms a part of the mechanism for projection. In fact, no adequate explanation has yet been offered to account for the projectile force. The same development and forcible discharge of basidiospores occurs in many of the higher Basidiomycetes (Buller, 1922, 1924).

FIG. 121. — Development of the basidiospore of *Puccinia graminis:* as the spore enlarges at the point of the sterigma a drop of water appears. When the spore is full size, it is shot away and carries the drop of water with it. (After Buller, 1924.)

The distance to which spores from cupulate and caeomoid aecia can be ejected vertically is found to be from 4 to 15 mm., and horizontally about half as much further, according to the species and the size of the spores. In *Puccinia graminis* the maximum height to which aeciospores are discharged is 7 to 8 mm. (Buller, 1924). Sometimes the aeciospores are not only discharged singly but in masses of as many as 150 spores each (Buller, 1924). Aeciospores of *P. podophylli* have been found to be projected 1.5 mm. horizontally, and of *Gymnoconia interstitialis* 1.1 mm. while in both cases the vertical discharge is about 1 mm. (Dodge, 1924b). *Kunkelia nitens*, the microcyclic form corresponding to the latter species, possesses waxy spores, and only rarely are any of them projected out of the sorus.

It has been found that thickenings over the pores of the aeciospores of *Gymnotelium myricatum* (*Gymnosporangium myricatum*) (Dodge, 1924a) and *Puccinia podophylli* (Dodge, 1924b) greatly aid the expulsion of the spores by serving as a fulcrum against which the elastic walls

react (Fig. 122). Such pore-thickenings are not formed in *Gymnoconia interstitialis*, but the spores in this species are nevertheless ejected with considerable force.

All spores so far shown to be forcibly dislodged have moist or sticky surfaces, but not waxy. No tests of roestelioid and peridermioid aecia have been made, but it is probable that in the former (Fig. 74) the hygroscopic opening and closing of the peridium (Lloyd & Ridgway, 1911; Reed & Crabill, 1915), and in the latter, the dropping away of the peridium, constitute the chief aids to the dislodgment of the spores in many of the species. It is also probable, no tests having been reported, that uredinia of the ordinary sort and stylosporic aecia have slight, if any, mechanical aids to effect the discharge of their spores. In these cases the spores are borne singly on stalks and are usually dry and highly pulverulent, which permits them to be readily scattered by the wind.

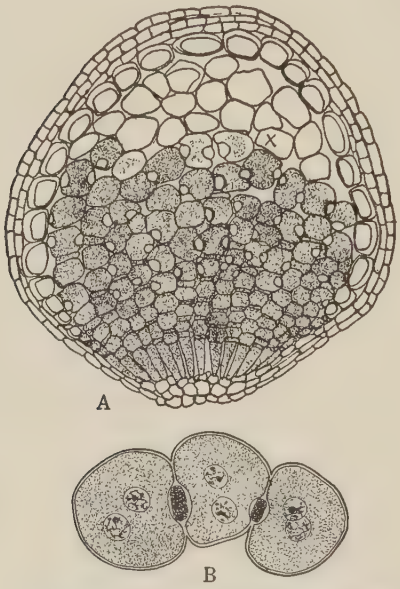


Fig. 122. — Aecium of *Gymnotelium myricatum*, showing thickenings between the spores: *A* diagrammatic section of mature aecium; *B* detail of thickenings between the spores. (Dodge, 1924a.)

Movement due to gravitation. — The fall of spores in still air has been shown by Buller (1922) to follow approximately the same law of acceleration that applies to other small bodies. Very few tests have been made with rust spores. McCubbin (1918) ascertained that it took up to five minutes for urediniospores of *Cronartium ribicola* to fall 8 feet (24 dm.) in still air, or about 8 mm. per second. Such spores average 20–30μ in diameter. Buller (1924) from his studies estimates that hymenomycetous basidiospores will fall from 1 to 3 mm. per second. They are about one-fourth to one-eighth the size of urediniospores, and judging from the above data fall about one-fourth as rapidly. This action of gravitation, although seemingly very small, should be taken into account in a careful study of spore dispersal. McCubbin (1918) calculates that urediniospores of *Cronartium ribicola* if "set free 8 feet above the surface of a level plain, a 30-mile breeze would carry them

$2\frac{1}{2}$ miles before they could sink to earth, or if liberated from a small hill 32 feet above the plain they would be carried 10 miles by the same breeze before being deposited."

Convection currents. — Observations made by Falck (1904) showed that the distribution of spores in a closed chamber was not due to the force of ejection alone, but also to imperceptible movements of the air brought about by slight differences of temperature. Such convection currents, common in all gases and liquids, must be always present under natural conditions of spore production, and must aid materially in spreading the spores, even in a seemingly quiescent atmosphere.

Light and heavy winds. — The spread of rusts from one host to another by means of wind-borne spores has doubtless had general recognition for a long time. A. P. DeCandolle in France and Sir Joseph Banks in England writing at the beginning of the nineteenth century take this method of spore distribution for granted. It was not until comparatively recently, however, that any direct proof was recorded. Ward (1882) was the first to demonstrate the action of the wind in his studies of the coffee disease (*Hemileia vastatrix*) in Ceylon, by catching the urediniospores on slides smeared with glycerine.

The wind is obviously the most important agency in the spread of rust spores under natural conditions. Spores that become pulverulent in the sorus are easily taken up even by light air currents, and it is notable that nearly all such spores, whether aeciospores, urediniospores, or teliospores, have their surfaces roughened by echinulate or verrucose prominences, while spores that are not easily dislodged from the sorus, like many teliospores, have a smooth surface. Roughness evidently assists in attaching the spores to the surface of leaves or stems of plants on which they alight, and possibly in making them more buoyant.

In autumn and winter the wind often carries dry fragments of plants considerable distances over snow or frozen ground. Attached spores as well as seeds become distributed in this way (Lind, 1927).

Teliospores remaining in contact with the plant on which they grew germinate *in situ*, yet the basidiospores thus produced receive the same or even greater service from the wind as a distributor than the larger pulverulent spores. Basidiospores are mostly smooth, and they doubtless possess their chief advantage in securing a hold on plant surfaces by their minuteness and by surface moisture or a mucilaginous secretion (Waterhouse, 1921).

It has been a matter of common observation for more than a century

that wheat fields bordered by barberry hedges are rusted less and less in proportion to distance from the hedge, and similar observations are not uncommon for other grain rusts and for fruit rusts and other kinds. This fact of relation to source of infection is utilized in many cases to detect the probable alternate host of a heteroecious species (Arthur, 1902c), and also to locate the source of injury to a crop. It was used to condemn the barberry bush more than half a century before the aecial host of wheat rust was definitely determined.

Marshall (1787, p. 359) made the observation that a bush of barberry, which he had set in the middle of a twenty-acre field of wheat in the spring of 1782, produced harmful effects, although he was unable to detect the active agent. "About the barberry bush," he writes, "there appeared a long but somewhat oval-shaped stripe of a dark livid colour, obvious to a person riding on the road at a considerable distance. The part affected resembled the tail of a comet, the bush itself representing the nucleus, on one side of which the sensible effect reached about twelve yards, the tail pointing towards the southwest, so that probably the effect took place during a northeast wind. At harvest the ears near the bush stood erect, handling soft and chaffy; the grains slender, shriveled and light. As the distance from the bush increased the effect was less discernible, until it vanished imperceptibly." Many similar observations by Marshall and others are on record, made during the latter part of the eighteenth and beginning of the nineteenth century, some of which are cited by Plowright (1889).

A specially interesting case, due to exclusion of modifying influences, is reported by Dietz (1923) from north-western Iowa. Oat rust (*Puccinia coronata*) was spread by aeciospores from a hedge of *Rhamnus cathartica* (Fig. 177) to a distance of $1\frac{1}{2}$ miles, but most of the aeciospores dropped within 80 feet of the hedge, as indicated by the degree of infection. After the urediniospores formed and had become effective in aiding the distribution the rust was found more than 50 miles away, no plantings of Rhamnus intervening.

The spread of the white-pine blister rust (*Cronartium ribicola*) has received much attention in America, and results have been summarized (Spaulding, 1922), showing that aeciospores have apparently caused infection of Ribes at a distance of a few hundred feet up to 7 miles. More recently Pennington (1924) offers observations to indicate that aeciospores of this species under exceptional conditions may be carried 150 to 200 miles and cause infection.

In Virginia, Schneiderhan (1926) studied the spread of basidiospores

from the cedar rust (*Gymnosporangium juniperi-virginanae*). He found that 77 per cent of the leaves on apple trees were infected at a distance of 1½ miles from the rust-bearing cedars. The average intensity was 11.5 spots per leaf. At greater distance infection decreased correspondingly. At three miles 20 per cent of the leaves were infected, with an average of only 0.32 spots per leaf. Other records for these and other species might be cited to the same end.

Since 1882 (p. 165) many persons have studied the movement of wind-borne spores by exposing surfaces coated with gelatine, glycerine, or vaseline, or by using spore-traps through which the air is drawn for a definite time and the spores caught upon cotton or a sticky surface. Gassner (1916) used this method effectively in the study of cereal rusts in South America. Spaulding (1922) cites the results obtained by several observers of the white-pine blister rust. The most conspicuous results have been obtained by Stakman (Stakman, Henry, Curran & Christopher, 1923) and Craigie (1926; Craigie & Greaney, 1927; Craigie & Popp, 1928), who have undertaken with their assistants to measure vertical distances by the use of aeroplanes.

The observations by Stakman's group were made over the great plains between Minnesota and southern Texas, and by Craigie's group in Canada from Manitoba to Alberta. In the southern area an abundance of spores was obtained up to 11,000 feet altitude. At 16,500 feet above Waco, Texas, in April, two urediniospores were taken of what appeared to be the leaf rust of wheat, *Puccinia rubigo-vera tritici*. Both aeciospores and urediniospores of *P. graminis* caught at 1,000 and also at 7,000 feet were germinated, showing that viable spores may be carried to great heights by winds. In the northern area many spores of *P. graminis* were taken at an altitude of 5,000 feet during the middle of August to the middle of September. At one time, on August 14 over Norway House, Manitoba, 259 urediniospores were obtained on 2 square inches of surface during fifteen minutes of exposure, and again on September 1 with the same conditions 116 urediniospores were obtained.

It is conceivable and partly substantiated that strong winds, cyclones and tornadoes may distribute rust spores to very great distances from their place of origin, as abundantly demonstrated for the much larger pollen grains of pines, which cause the so-called "sulphur showers." It is known that dust, volcanic ashes, etc., may be carried thousands of miles, even across oceans.

It has been a generally accepted theory that the initial infection of cereal crops in northern regions is usually brought about by uredinio-

spores carried northward by winds from southern regions where they make an earlier appearance. With *Puccinia graminis,* and some other species, there is no clearly evident method by which the rust survives the winter in cold climates when the alternate host is absent, as occurs in large sections of the great wheat growing areas of northwestern United States and western Canada. Much circumstantial evidence in favor of this theory has been adduced, but the evidence is somewhat conflicting. The clearest case appears to be that reported for the vicinity of Winnipeg, Manitoba, in 1925. A daily exposure of stationary slides during the last half of July showed that approximately 270 urediniospores of *P. graminis* fell during this time upon each square inch of land surface. The general epidemic of stem rust, however, did not appear in that region until about August 1, after which date approximately 1,100 urediniospores fell daily on each square inch of land surface under the same circumstances. When these and many other recorded data, both from stationary and aeroplane observations, are considered the conclusion seems strongly in favor of the idea that "the initial rust infections in Manitoba each year are caused by wind-borne spores from the south" (Craigie, 1926). A fact that also supports this conclusion is that the barberry bush has been practically exterminated from the wheat growing regions of Manitoba, and is a negligible factor in starting wide-spread rust epidemics.

Similar studies were made at the Amur Experiment Station at Blagoveshtshensk in eastern Siberia during the season of 1926 (Shitikova-Rusakova, 1927). Spore-catching apparatus was used, which was examined twice daily. Urediniospores of *Puccinia rubigo-vera tritici* were first observed on June 19, and the first uredinia on June 28, leading to the conclusion that the wheat was infected on June 16, immediately after two or three days of southeasterly wind. Another similar infection occurred on June 23. During the days immediately following the latter date the wind changed to the northwest and the urediniospores entirely disappeared from the air, but they reappeared on June 27 when the wind again blew from the southeast. The urediniospores of *P. graminis tritici* appeared nearly a month later and under similar conditions, with subsequent infection of the wheat.

Similar problems in Australia and Africa, where the hot, arid season as clearly interrupts the continuity of rust existence as does the winter season in northern climes, have not yet reached solution.

There are many reasons to believe, however, that long distance dissemination of rust spores through the air, although sometimes start-

ing epidemics, plays but a small part in the general geographic distribution of rusts, even of introduced species. The well known limitation of species within definite areas, endemic species, climatic factors, as well as the very slight chance of any spore that is carried a considerable distance from its origin finding favorable opportunity to introduce infection, restricts long-distance spreading by air-borne spores in most cases to occasional epidemic outbreaks.

In the far north, however, and probably to some extent farther south, heavy winds during the cold season may carry fragments of hosts together with adherent spores long distances over the smooth surface of frozen snow and ice. These may lodge against similar hosts, or be massed in favorable spots for the seeds to grow and obtain a footing, and infection be thus established when the next warm season opens. Perennial mycelium in a plant capable of being blown about and again taking root, like some species of Saxifraga bearing *Melampsora arctica*, may distribute the rust by its aecia, but far more often the distribution occurs through the adherent urediniospores or teliospores (Arthur, 1928). Such spread of rusts over arctic snow and ice may take place across great bodies of water, and even between continents (Lind, 1927), which in part accounts for the circumpolar distribution of many species.

Rains and streams. — As a disseminating agency water is rarely of much importance. No observations have been recorded in which it acts as an efficient distributor of rust spores. Rain drops may dash against exposed sori with sufficient force to scatter the spores over adjacent leaves or plants. Spores floating in the air are brought down by rain storms, and in connection with the wind can be distributed over considerable areas. Violent and continued storms, however, are more likely to wash spores from the air and from the surface of plants into the ground, and destroy or render them inefficient.

Water moving in mass, as in small or large streams, irrigating ditches, or freshets, may presumably carry the spores of rusts, but cases must be rare in which infection of suitable hosts results. Rust-covered débris, however, can be readily swept along and deposited where the conditions are favorable for the propagation of the species. An instance of this kind, due to the temporary overflow of a river, led to the discovery of the aecial host of the corn rust, *Puccinia sorghi* (Arthur, 1904a).

Animal agencies. — Insects have long been recognized to be of greater or lesser importance in the spread of rusts. They carry the spores about on their rough bodies in the same manner as they transport pollen grains. Spores of numerous species, especially the aeciospores

and urediniospores, provide an acceptable food for many kinds of insects, and especially for their larvae. Although in this way they destroy the spores and to that extent decrease the spread of the rust, yet at the same time they effectively add to its distribution by scattering the spores that become attached to the sides, legs, and other parts of their bodies. The larvae of a neuropterous insect, *Smynthurus* sp., were observed by Webster (1890) in Indiana to feed on the urediniospores of *Puccinia rubigo-vera tritici* on wheat leaves, and doubtless to carry the spores to other plants. Several species of dipterous larvae of the family Cecidomyiidae were seen by Cobb (1892, p. 188) in Australia to feed on urediniospores from the rust of wheat and of a score of other plants, and also on teliospores from the rust of a marsh mallow. A careful count was made of the spores attached to the larvae of *Diplosis* sp., one of the cecidomyiids which were crawling over rusted plants, and showed an average of 1,121 spores on the back of each larva. The spores were found to be in germinating condition. These larvae in moving over clean paper or glass each dropped about 250 spores in a distance of one inch, requiring two or three minutes of time. Thus it was positively demonstrated that such larvae are capable of spreading the spores of rusts. To demonstrate further if they could also communicate the rust to healthy plants an ingenious safe-guarded experiment with the same kind of larvae bearing urediniospores of *Uromyces bidenticola* gave infection on *Bidens pilosus* (Cobb, 1892). The honeybee (*Apis mellifica*) sometimes gathers spores of rusts (Lang, 1901) in the same manner and doubtless for the same purpose as it customarily takes pollen grains, and must necessarily distribute them more or less effectively. Conspicuous instances of such action are recorded from California (Bessey, 1901) in which urediniospores of *Melampsora* sp. were gathered from *Populus* sp., and from central Texas (Lang, 1901) in which the spores of *Caeoma nitens* from *Rubus trivialis* were packed upon the legs of bees without admixture of other material. During the season of 1918 in Essex County, New York, urediniospores of *Cronartium ribicola* from *Ribes* sp. were observed (Snell, 1919) on the bodies of over 40 species of insects, partly larvae and partly adults of many families, and also on spiders and slugs. Basidiospores were found on two species of ants. Aeciospores were found on a scarabaeid beetle (*Serica sericea*), taken on leaves of *Ribes rubrum* one mile from source of the spores. In ten experiments positive spread of the rust to healthy plants of *Ribes prostratum* by such insects, both larvae and adults, bearing urediniospores, was demonstrated. The larvae of the gypsy moth (*Porthetria dispar*)

have been found by actual count (Gravatt & Posey, 1918) to bear individually from 1,120 to 28,320 aeciospores of *Cronartium ribicola* on their bodies. These larvae feed abundantly on the under surface of Ribes leaves, and doubtless carry infection to nearby plants and when borne by the wind to plants many miles away. It is a common experience of those who carry on culture experiments in greenhouses that thrips, very small and exceedingly active insects, cause much annoyance by eating out the sori and also transporting the spores. Observations in Texas (Johnson, 1911a) have shown that they disseminate the urediniospores both of leaf and stem rust of wheat, and that when these spores are carried among the glumes a high percentage of sterility ensues, presumably due in part to the growth of the rust.

The visit of insects to secure the sweet exudation from pycnia of many species of rust, especially including two common species of Gymnosporangium and those of some common cereal rusts, was studied exhaustively by Ráthay (1883) at Klosterneuburg, Austria. He identified 135 insect visitors belonging to the Coleoptera, Hymenoptera, Hemiptera and Diptera, nearly half being included in the last group. Undoubtedly the attraction offered to insects by the nectar of the pycnia is an aid to the dissemination of both the associated pycniospores and aeciospores, although this may be no indication of its purpose. It has been proved experimentally, however, that insects do play an important rôle in transporting the pycnial products from one colony of pycnia to another of the same species of rust, and in so doing hasten the formation of aecia (Craigie, 1927b).

Usually, as in the above instances, the roughness of the spores provides an important means by which they are kept in place on the insects. Magnus (1891) suggests that the gelatinous layer in the wall of the pedicel of some teliospores when swollen and ruptured by absorption of moisture may stick the spores to the passing insect, and thus serve as an adaptation for spore dissemination (*e.g.*, Diorchidium, Phragmidium).

Other small animals beside insects are often a menace to the growth of rusts in the greenhouse. Not only do they eat the spores, but in moving about have been found to distribute them. Observations were made by Gravatt and Marshall (1917) on slugs (*Agriolimax agrestis*), sow bugs (*Armadillidium vulgare*), and snails (*Subulina octona*), in connection with *Cronartium ribicola*. The excreta from these animals, and also from a number of insects, were found to contain many spores, but only a small percentage both of the urediniospores and teliospores was viable

Birds may carry rust spores, but they are probably not important agencies in the spread of rusts except occasionally over barriers, or locally. Squirrels, porcupines, cattle, sheep, horses, dogs, and other animals may give unconscious aid to the dissemination of the spores of rusts.

The human agency. — Man has brought about the spread of many rusts for great distances, and has been particularly effective in spreading unintentionally species of rusts which cause him financial loss, namely those which attack his cultivated crops. His ships have carried rusts across every ocean, and his trains, automobiles, and other transportation facilities have penetrated most of the inland areas.

Transplantation of host. — Rusts may be distributed both in the form of mycelium within the host, and by the accompanying spores. *Cronartium ribicola* is known to have been imported from Europe into North America in 1908 upon white-pine seedlings (Spaulding, 1909), although it probably came into the northeastern United States fully ten years earlier (Spaulding, 1922). It has been known in Europe for sixty years or more. Gymnosporangia may also be spread as mycelium with shipments of Juniperus, which is doubtless the way in which *G. koreaense* and *G. photiniae* (*G. japonicum*), both Asiatic species, gained access to the east and west coasts of North America. Another instance of a similar kind is that of *Endophyllum sempervivi*, a microcyclic rust, first noticed in North America in 1917 in the vicinity of New York City.

The rust of chrysanthemums (*Puccinia chrysanthemi*), a native of Japan, has been transported upon cuttings or small plants nearly everywhere that these popular flowers are grown. It was observed in England in 1895, in the United States in 1896, in northern Germany, France and Denmark about 1897, in Switzerland in 1900, and in Australia and New Zealand in 1904. In the same way the rust of the carnation (*Uromyces caryophyllinus*), a native of southern Europe, where it was recognized by botanists as early as 1789, a heteroecious rust that is usually spread locally by its urediniospores, was first noted in the United States in 1891, and now greenhouses generally throughout the country show the rust, unless special care is exercised to guard against it. It reached Australia in 1896.

The snapdragon rust (*Puccinia antirrhini*) presents a similar instance. It is spread by cuttings or seedlings from infested greenhouses. It is a native in the mountains of California. It was first observed in the vicinity of San Francisco in 1879[1] on the exotic *Antirrhinum major*,

[1] A specimen in the Farlow Herbarium at Cambridge, Mass., bears the legend "Santa Cruz, Calif., 1879. Anderson."

but not given a name for nearly two decades (Dietel, 1897b). The first detailed record was made six years later (Blasdale, 1903). Within a few years it had spread northward to British Columbia and southward to southern California and somewhat more slowly eastward. The first record of its occurrence east of the plains was in 1913 in the vicinity of Chicago (Peltier & Rees, 1914). It spread so rapidly that in two years it had reached the greenhouses of the Atlantic coast, and not long afterward was reported northward into eastern Canada and southward to the Gulf of Mexico. In 1922 it was observed in Bermuda.

Another instance of the introduction of a rust with its living host is worth mentioning, for in this case the establishment of the rust was promptly checked and injury averted. In 1903 a Wardian case containing seedling coffee plants was received at Mayagüez, Porto Rico, from the Dutch East Indies by way of Holland. The presence of *Hemileia vastatrix* on the plants was detected by Mr. O. W. Barrett, the government botanist, and after sending samples of the affected leaves to Washington, all the coffee plants except four or five were burned, together with all packing and refuse that came with them. The few reserved plants were carefully cleaned, disinfected, and put under observation in a protected case. Thus ended a critical episode for the coffee industry in America.

The coffee rust, which is propagated by urediniospores, is doubtless a native of eastern and central Africa, where it is known on wild and semi-wild species of the genus Coffea, as well as on the chief coffee plant of commerce, *C. arabica.* It first became an economic problem in the epidemic outbreak in Ceylon in 1868. From that center it gradually spread to all the great coffee-growing regions to the eastward and well into the Pacific, at least as far as Samoa, which was reached in 1894. The movement coincides with the introduction of coffee varieties into the British, Dutch and French colonies. That the dissemination of spores by wind has played an insignificant part, if any, in this case, is clear from the fact that while the rust is common in the central Belgian Congo it has never spread to the west coast of Africa, although host-conditions and climate are favorable. That it has not reached the great coffee areas of North and South America probably is due to the mode of transportation of the host free from leaves.

Alien species and their spread. — Rusts introduced into new regions have in the past seldom received attention unless they caused marked damage to cultivated plants. We cannot now determine how many rusts of a region are of alien origin. It is evident that if *Cronartium*

ribicola and *Puccinia malvacearum* had been introduced into North America many years earlier, we should be led to believe, from their present wide distribution upon native plants, that they were indigenous. McAlpine (1906) has presented data indicating that 31 of the 161 rusts of Australia are introduced. He considered that *Puccinia graminis* reached Australia in 1825. The Australian rust-flora includes 30 species belonging to the form-genera, Caeoma, Aecidium and Uredo, but only one of these form-species is placed with the introduced species. These data, in view of the comparatively recent settlement of the country, are probably more nearly complete than could be presented for any other large land area. Cunningham (1923-26) finds a corresponding number of introduced species in New Zealand.

Below are listed the rusts which appear to have been introduced by man into North America. The number is small (40, only 4 per cent of the rusts of the continent) and cannot be a complete list. The number of introduced species clearly is not related to the number of rusts present in a country, nor upon its size, but upon its commerce with foreign lands. Introduced species should approximate a constant number for similar areas with similar time and extent of interchange of products from elsewhere in the world.

RUSTS INTRODUCED INTO NORTH AMERICA

Coleosporium senecionis (Eur.)
— sonchi-arvensis (Eur.)
Melampsora euphorbiae (Eur.)
Cronartium ribicola (Eur.)
Phragmidium disciflorum (Eurasia)
Gymnosporangium koreaense (Japan)
— photiniae (Japan)
Uromyces appendiculatus phaseoli (Eur.)
— appendiculatus vignae (Asia)
— betae (Eur.)
— caryophyllinus (Eur.)
— coluteae (Eur.)
— dactylidis (Eur.)
— striatus (Eur.)
— trifolii (Eur.)
Puccinia acetosae (Eur.)
— anomala (Eurasia)
— arachidis (S. Amer.)
— asparagi (Eur.)
— bardanae (Eur.)
Puccinia carthami (Eurasia)
— chondrillina (Eur.)
— chrysanthemi (Japan)
— coronata avenae (Eur.)
— cyani (Eur.)
— cynodontis (Eur.)
— glumarum (Eur.)
— graminis phlei-pratensis (Eur.)
— graminis tritici (Eurasia)
— holcina (Eur.)
— lapsanae (Eur.)
— malvacearum (Chile, *via* Eur.)
— melanocephalum (China)
— porri (Eur.)
— rubigo-vera agropyri (Eur.)
— rubigo-vera secalis (Eurasia)
— rubigo-vera tritici (Eurasia)
— suaveolens (Eur.)
— variabilis (Brit. & Scand.)
— vincae (Eur.)
Endophyllum sempervivi (Eur.)

It will be noted that most of the above rusts occur upon cultivated plants, especially upon the cereals. Races or varieties are treated the same as morphologic species, for those included in the list are subject to like restrictions in their geographic distribution. A few species are upon introduced weeds.

A sharp distinction must, in general, be drawn between the mode and rapidity of distribution shown by rusts of native plants and rusts of cultivated plants and weeds. Indigenous rusts, like indigenous vascular plants, doubtless spread slowly, and indeed have often seemingly evolved and spread along with the evolution and spread of their hosts. A weed, or a cultivated plant, may spread or be spread with great rapidity, and the rust on such a plant, when introduced, may soon reach the range of the original host and of closely related ones.

The rapid spread of a rust over long distances may be brought about by the débris accompanying the seeds. In the case of cereals the chaff and fragments of leaves and straw may bear teliospores, which could start the rust in an uninfested locality, provided a suitable alternate host were present, or possibly some viable urediniospores might be thus transported. In autoecious rusts the method is simpler. Thus the hollyhock rust (*Puccinia malvacearum*) is doubtless carried on the involucre or other dried parts of the flower that accompany the seeds, and sometimes even upon the seeds themselves (Taubenhaus, 1911). In other cases the teliospores are on packing material. Instances where the rust is distributed along with the living plants have already been given.

It is possible that the spread of *Puccinia asparagi*, the rust of asparagus, over long distances in North America has been brought about by the packing or the soil that accompanied the roots, rather than by wind-borne spores. It was first observed in North America near the Atlantic coast between New Jersey and Massachusetts in 1896 (Halsted, 1898a). The next year it was reported as far as South Carolina to the southward and Vermont to the northward. In 1898 it made its appearance in a number of localities as far westward as Michigan. In 1899 it was seen in Illinois, Ohio, and even as far as Kansas. By 1900 it had spread throughout the eastern United States and reached the dry plains extending from the Dakotas to Texas. The leap of 1200 to 2000 miles across the semi-arid and mountainous regions of the west was apparently accomplished at the same rate of advance as shown in eastern states, for it appeared in California from Sacramento southward in 1901. There is some evidence to show that the asparagus rust had been seen

in California many years before the date mentioned, but if so, it had not invaded any of the large commercial centers (Smith, 1905). A very notable feature of the remarkable spread of this rust from the Atlantic seaboard to the Pacific within the brief period of six years is that it usually first appeared in each locality in large fields and in epidemic abundance. It is, therefore, difficult to understand how this rapid advance could have been accomplished in any other manner than by the shipment of plants. The purchase of asparagus plants from eastern dealers has been the customary way with western cultivators to establish or replenish a field of asparagus.

Another rust has an interesting history, and illustrates still another method of dissemination. The mallow rust, *Puccinia malvacearum*, was first recorded in 1852 as part of a collection of plants made in Chile by Montaigne. It apparently started on its travels by reaching Australia in 1857. Its next appearance was in Spain in 1869. Its movement through Europe was rapid, invading France in 1872, Germany and England in 1873, Italy in 1874, Switzerland in 1875, Austria in 1876, Greece in 1877, but did not reach Sweden until 1887, and Finland until 1890. It appeared in South Africa in 1875, but did not reach North America until 1886. The hollyhock, *Althaea rosea*, and the common mallow, *Malva sylvestris*, are the hosts that lead in aiding the distribution. As these plants are rarely shipped from place to place, but are propagated from seed, it is highly probable that the distribution of the accompanying rust, which is a microcyclic form, has been brought about by the spores attached to involucral bracts, calyx, or other parts of the plants that may be intermixed with the seeds. The mallow rust was introduced into North America with seed of *Malope grandiflora* imported from Europe (Farlow, 1886). Sori may occur on both the carpels, each of which contains a single seed, and on the calyx or involucral bracts. It has been demonstrated that plants grown from encapsuled seed of *Malva rotundifolia* free from débris can become rusted (Taubenhaus, 1911). In some species even seeds themselves may at times bear rust pustules, and transmit the fungus to seedling plants. This has been demonstrated for the autoecious species, *Uromyces proëminens* and *U. dictyosperma* (Mains, 1922b).

Factors which lessen the dissemination of rusts. — The factor that acts most strongly as a check upon the abundance and spread of the rusts is that of unfavorable or unseasonable climate. Excessively arid or cold regions support few rusts, and in consequence not many species are found in deserts or far northward. Adaptation in many

species permits the survival of spores or mycelium through intermittent periods unfavorable to growth of the fungus, such as the winter season in temperate climates or the dry season in tropical climates. But unusual severity or extension of such periods may prove very destructive, and not infrequently cause the scarcity or total disappearance of a species from certain localities. But even in otherwise favorable seasons warm weather unusually early in the spring often causes teliospores to germinate in advance of the appearance of suitable alternate hosts, and thus come to naught. This is especially true with rusts on Carex, which in most instances respond readily to warm and moist weather in spring.

The consumption of spores by insects, especially by their larvae, has already been mentioned (p. 170). Larvae are frequently observed in a dried condition on fungous material collected from all parts of the world, especially in the sori of aecia and uredinia. This is one of the many indications that the depredation of insects and other small animals cause the destruction of no inconsiderable percentage of the spores of rusts. Fungous parasites also prey upon the rusts and greatly inhibit their reproduction. *Darluca filum* and *Tuberculina persicina* are common cosmopolitan parasites of the rusts, found especially in aecial and uredinial sori. Apparently some species of rusts are more susceptible to parasitic attack than others. *Uromyces junci* and other species on Juncus are especially invaded and often to such an extent that the formation of teliospores is much restricted, and the same is true of some species of Puccinia on Carex. Other parasitic fungi have been described belonging to a number of genera and many species, which attack or inhibit rusts (p. 197).

GEOGRAPHIC DISTRIBUTION

Incompleteness of basic knowledge. — There are two prominent limitations at the present time to the study of the geographic and phylogenetic distribution of the rusts. As set forth in the chapter on classification, no agreement has yet been reached among uredinologists regarding the definition of species or the practice to be followed in their establishment. The early method, which still persists to some extent, was based on the necessity of giving a name to each form as found, without waiting to ascertain the full cycle of which the form is a part. This method has introduced many more names than the actual number of species represented. Even if the need of keeping in view the different stages of a species is recognized, there is the further

difficulty in many cases of telling whether forms that have received names should be ranked as species or as varieties or races. Furthermore, identically the same species from different regions sometimes appear under two or more names, unwittingly given by different authors. The numerical comparison of the rusts in different regions is therefore most unsatisfactory at present, even with the best possible evaluation of the recorded names.

The other difficulty in the study of distribution is the meager knowledge of the rusts in many regions. Doubtless Europe and North America are the best explored portions of the earth for rusts, but the large number of new species now being brought from parts of Central America and the West Indies indicates the incompleteness of knowledge of areas in which much collecting has already been done. In the southwestern United States, parts of Mexico, Yucatan, Honduras, northern Guatemala, Salvador, and Nicaragua, there are great geographic areas in which the rust-flora is almost wholly unknown. This is only noting the large blank spaces of North America, but even in the best known regions new species are constantly being brought to light. A similar condition exists in Europe, while in South America, and the best known parts of Asia and Africa, a still greater disparity exists between the known and unknown conditions of the rust-flora. Then there is the enormous expanse of China, Siberia, the northern plateaus of the Himalayas, and adjacent regions, forming for the most part a *terra incognita* in this regard. Furthermore, the strange forms of rusts, as viewed from the present north-temperate standpoint, which occur in the southeastern peninsulas of Asia, and in the Australian, Philippine and other insular regions of the Pacific Ocean, can scarcely be brought into a present day discussion of distribution.

Species that are comparable. — It is self-evident that in making comparisons the objects to be compared should be of the same kind or nature, and that parts should not be set off against wholes. With the rusts many species have unlike ways of manifesting themselves, one of the greatest differences being in the number of kinds of spores borne during the period of a single life-cycle. All the macrocyclic rusts have two mycelial states, each giving rise to two or three kinds of fruiting structures, while the microcyclic rusts have but one mycelial stage in their life-cycle, producing only one kind of active fruiting structure. In speaking of species in the present connection it will be understood that species having actually or potentially aeciospores, urediniospores and teliospores will be considered in a different group

from the species capable of producing only one kind of effective spore. It further will be understood that in listing species the names applied to form-genera, such as Aecidium, Uredo, Peridermium, etc., together with those given to forms so imperfectly known that it is uncertain whether or not more than one mycelial stage is produced, will be omitted unless statement is made to the contrary. However, it is so recent that mycologists have given attention to life-cycles in announcing their observations that many slips are likely to be made in assorting recorded names.

Abundance of individuals. — Rusts may be found nearly everywhere that plants grow. They are among the most common and easily recognized of the microfungi. The abundance of rusts upon certain cultivated crops, such as the cereals, is a world-wide phenomenon of great economic importance. Many wild plants also bear a comparable abundance of various species of rusts: sedges, wild grasses, roses, composites, and many others can be found bearing rust sori during part or all of the growing season. The only parasitic fungi that compare with the rusts in ubiquity and abundance are certain *fungi imperfecti*, and these are usually less noticeable than the rusts.

Truly comparable data for rusts from fairly large areas in different parts of the world are not available. But in general it may be asserted that the larger the area the greater the number of species found within it, provided that phenologic conditions do not unduly restrict the number and kinds of hosts, as in the far north, and that equal attention has been given to exploration. This statement is well borne out by a study of Tables 8 (p. 182) and 9 (p. 186), for the areas there included.

Indigenous and endemic rusts. — Any area bearing vascular plants, whether a square meter or a continent, may sometimes be found to contain introduced, indigenous, and endemic rusts. Introduced or exotic species, which have already been considered (p. 173), are those brought in "artificially," that is, chiefly by the agency of man. Endemic or local rusts are those which occur only in a certain area, whatever their origin, while indigenous or native species are those which have dispersed "naturally" into an area, but which may occur also outside of that area. It is evident that the terms endemic and indigenous are relative. A rust endemic in a large area would be indigenous to an area covering part of its range. Obviously the smaller the area, the lesser the percentage of endemic rusts, except that the greater the isolation of an area, the greater the likelihood that endemic rusts may occur. The interpretation of endemism must necessarily vary as our

knowledge of distribution increases. A rust now considered to be endemic to North America may later be found in South America, whereupon the species becomes indigenous to each continent. The various rusts "known only from the type locality" may, so far as we know, be considered as endemic to the area in which they were collected, perhaps only a single host on a square foot of ground. Furthermore, time constantly changes the relation; the range of a rust may increase or decrease. We ordinarily interpret the range of a rust from data or specimens covering a considerable period of time, and even then our conception of the range may be too small, or it may be too large, for we assume that a rust found in a locality will persist there, as it usually, but not always, does. It is only in regard to important rusts of economic plants that we have for any continent approximately adequate data regarding the total range, and of the fluctuations from year to year.

Of 1000 species of rusts of known life-cycles in North America approximately 600 can be rated as endemic. These are distributed among the larger genera as follows: Puccinia 344, Uromyces 98, Ravenelia 54, Gymnosporangium 25, Coleosporium 23, Phragmidium 11, Melampsora 6, Cronartium 4, and all smaller genera together 35.

Climatic zones in North America. — The completion of the record for the Uredinales of North America (Arthur, 1907–27) permits an intimate analysis of the rusts found on the North American continent and adjoining islands, an area which extends from the Atlantic Ocean to the Pacific and from a few degrees north of the equator to the Arctic Ocean. By a study of the distribution of individual species a division of the area into three main climatic zones is possible, which may be designated as hot, cold and intermediate or as tropic, boreal, and temperate (see map, Fig. 123). The boundaries for these regions do not coincide with those usually drawn for climatic or biologic purposes, but serve the needs for a study of the north and south diffusion of the rusts. There are marked deviations from the general trend of the division lines at their western ends. In the southwestern region a loop occurs, which is doubtless occasioned by arid conditions, while in the northwestern region the similar loop is occasioned by high mountains. In addition to these deviations the sweep along the coast of Alaska indicates a climate between the mountains and the ocean tempered by the Japanese current.

Roughly speaking the tropic zone as here indicated extends from near the equator to about 6 degrees of latitude north of the tropic of Cancer, most of which is more accurately designated as sub-tropic, while the

boreal zone includes the arctic region proper and about 30 degrees of latitude south of the Arctic Circle, most of which would usually be designated as sub-arctic. The summits of high mountains, including those of the White Mountains, and those above 10,000 feet (3,000 meters) in the western mountains, possess a rust-flora which also belongs to the boreal area, but they are not indicated on the map. The temperate or intermediate zone has been more thoroughly surveyed for rusts than the others, and consequently would show to somewhat undue advantage in an accurate statistical comparison.

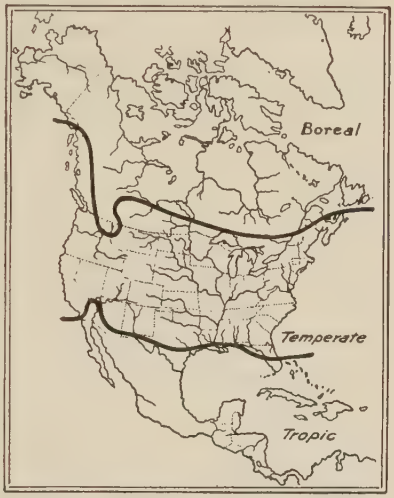


FIG. 123. — Climatic zones in North America as indicated by the distribution of the rusts. (Original.)

GENERAL DISTRIBUTION FROM NORTH TO SOUTH. — Owing to the labor involved in assorting data strictly in accordance with the three divisions indicated on the map, Table 7 presents an approximation. All of Alaska and Canada, except the province of Nova Scotia, are included in the boreal zone, and the central area is extended to the southern boundary of the United States. The data do not include about 200 names of "species" whose full life-cycles are not known, most of them standing under Aecidium and Uredo. When a species extends across a boundary, it is counted for each area, hence the large totals. Only a few more than 1000 species are involved in the data.

TABLE 7 — RUSTS IN THREE CLIMATIC ZONES OF NORTH AMERICA

	Macrocyclic Species	Microcyclic Species	Total Species*
Canada, Newfoundland and Alaska	170	51, or 23%	221
United States and Nova Scotia	543	126, or 19%	669
Mexico, Central America and West Indies	435	75, or 15%	510
Summary	1148	252, or 18%	1400

* Excluding unconnected species belonging to form-genera, but including species from adjoining areas.

After all due allowances are made for imperfections in the data it remains evident that the largest number of species is found in the temperate zone, and smaller numbers occur both northward and southward. This distribution is equally true whether the species are taken without assortment or separated into macrocyclic and microcyclic groups.

Distribution of the larger genera. — The larger genera of North America in their north and south distribution show wide diversity. In Table 8 the thirteen largest genera have their species separated by zones. As the microcyclic species of a genus as a rule fall within the geographic limits of the macrocyclic species of the same genus the two groups of species are here united.

Table 8 — Rusts of North America by Genera in the Three Climatic Zones

	Genus	Boreal Area	Temperate Area	Tropic Area	Total Species
Melampsoraceae	Coleosporium	1	21	16	30
	Melampsora	8	12	3	13
	Pucciniastrum	7	10	2	10
	Cronartium	4	6	2	6
	Uredinopsis	3	6	1	6
	Hyalopsora	1	4	0	4
	Milesia	2	2	3	6
Pucciniaceae	Puccinia	130	358	261	536
	Uromyces	28	108	70	152
	Ravenelia	0	22	44	59
	Gymnosporangium	5	33	2	33
	Phragmidium	13	16	2	16
	Uropyxis	0	6	5	10
Summary		202	604	411	862

The northern extension of these genera is fairly well known, but owing to imperfect knowledge of the rust-flora of South America, the southern limits of the genera, when extending beyond the confines of North America, can not be stated with much certainty except for Puccinia and Uromyces.

The genus Coleosporium occurs in considerable abundance along the

mountains through Central America and the Andes southward as far as Chile, although no aecial collections have been taken south of the United States, unless some unattached foliicolous forms of Peridermium in Mexico and Guatemala belong here. The genera that are more particularly northern in character are Melampsora, Pucciniastrum, Cronartium, Uredinopsis, Hyalopsora, Gymnosporangium, and Phragmidium. The more tropical genera are Milesia, Ravenelia, and Uropyxis. The two remaining genera, Puccinia and Uromyces, may be considered cosmopolitan, and limited chiefly by area.

Studying Table 8 in regard to the two great families of the rusts, Melampsoraceae and Pucciniaceae, it is seen that passing from south to north the percentage of Melampsoraceae is 7, 10 and 13 per cent, while correspondingly the percentage of Pucciniaceae is 93, 90 and 87 per cent, showing that in general the Melampsoraceae increase toward the north, while the Pucciniaceae increase toward the south.

Distributional relation of uromyces and puccinia. — The total number of species under Uromyces in Table 8 makes 22 per cent of the total number of species under the two genera of Uromyces and Puccinia combined. In a computation made by Dietel (1911a), based upon the first and second volumes of Sydow's "Monographia Uredinearum," the percentage for America (including both North and South America) was found to be 25 per cent, for Europe 24 per cent and Asia 26 per cent.

It seems that taking the world at large, or even any considerable portion of its land surface, the number of species of Uromyces is likely to be about one-fourth of the total Uromyces-Puccinia species. Pursuing the inquiry somewhat further we learn from Table 8 that there is a smaller percentage of Uromyces both in the colder northern third and warmer southern third of North America than in the middle temperate portion. The figures amount to 13 per cent for the north, 20 per cent for the south, and 24 per cent for the middle.

Augmentation of the life-cycle. — The abundance of uredinia in the warmer regions is a phenomenon attested by all collectors. Among both autoecious and heteroecious species the prolonged and conspicuous production of uredinia is noticeable, and in many instances aecia and telia are only occasionally formed. Of the 60 unconnected forms, given under the genus Uredo in the North American Flora (Arthur, 1924), 52 are known only in the tropic zone. In the well-explored island of Porto Rico 33 forms are listed under Uredo (Kern & Whetzel, 1926). The preponderance of unconnected forms of uredinia in the tropic zone can not be ascribed to the lack of detailed observation, for the 84 uncon-

nected forms listed for North America under Aecidium are equally distributed between the tropic and temperate zones, 42 being found in each.

The production of uredinia appears to be favored by the conditions, which exist in the warmer regions. It would be a hasty inference, however, to ascribe this adaptation to so simple a cause as temperature, for apparently the inciting factors bring about the preponderant or exclusive production of uredinia for some species in temperate regions, *e.g.*, *Puccinia poarum* and *P. iridis*, which form no telia between the Atlantic coast and the Mississippi valley, but produce telia in abundance in the Rocky Mountains westward to the Pacific coast. In cases like those cited the superabundant production of uredinia is of the nature of a lengthened or augmented life-cycle, in which an indefinite number of supernumerary generations of uredinia are interposed, but does not preclude the possibility of completing the cycle with telia and aecia when conditions are favorable.

Simplification of the life-cycle. — There is a general impression among uredinologists that the length of the cycle shows a tendency to shorten in proceeding from the equator toward the colder regions of the north. The shortening is manifested in different ways. There appears to be a lessened production of uredinia, as well as an increase in microcyclic species upon proceeding northward. It is also pointed out that a similar tendency is manifested in going from the base to the summit of high mountains.

By comparing the behavior of species in the tropic zone with those in the temperate zone and again with those of the boreal zone in regard to the general continuance of uredinial production it is readily seen that from a maximum amount in the tropics a decrease ensues toward the north. The explanation of this feature of distribution (p. 244) is a separate and complicated problem, which may be omitted here and in the similar cases to be taken up later, although many writers suggest that it is to be sought in the all-inclusive and many sided environmental action of climate.

Combined with the decrease in uredinia northward is the reciprocal increase in telial production. A conspicuous illustration is the boreal rust *Melampsoropsis empetri* (*Chrysomyxa empetri*), which occurs in abundance in the uredinial form on *Empetrum nigrum* in northern Europe, Asia and North America, extending southward to the summits of the higher mountains of New England and Switzerland at the southern limits of the host. The telia have been found only in Greenland and northern

Norway. More species with aecidioid aecia, especially heteroecious kinds, as compared with the autoecious species with uredinoid aecia, the so-called brachyforms, have been observed in the valleys and plains of Switzerland than on the mountain summits (Magnus, 1893). Although this can not be called a shortening of the cycle yet it seems to show a tendency in that direction. It has been pointed out that the abundance of uredinia is often conditioned on the nature of the foliage of the host and the length of time during the season when it can support the rust (Magnus, 1893; Ivanov, 1907; Morganthaler, 1910). The lessened abundance of uredinia in high altitudes was experimentally shown by growing *Puccinia pimpinellae* on *Pimpinella magna* in the Botanic Garden at Bern, Switzerland, and on the summit of the Faulhorn, over 2,000 meters (6500 feet) higher. Uredinia appeared a month earlier and continued a month later in the valley than on the mountain top (Fischer, 1908).

It is clearly evident from the above data, to which more of the same trend could be added, that a general tendency toward shortening of the life-cycle does occur in cooler climates and higher altitudes. The same proposition is further strengthened in tracing the distribution of microcyclic rusts.

Distribution of microcyclic species. — The increase of microcyclic species on mountain summits was first observed by Magnus (1893), who found that in the higher Alps of the Engadine, Switzerland, of 38 species of Puccinia 21 were microcyclic, or 58 per cent, which he ascribed to the shorter season for growth in the higher altitudes, both for host and parasite. The total rust-flora of Switzerland (exclusive of unconnected species of Aecidium and Uredo) was estimated by Fischer (1904) to be 350 species, of which 10 per cent were microcyclic, while the 76 species occurring above tree limits gave 46 per cent of microcyclic species.

The uneven distribution of microcyclic rusts was first observed by Johanson (1886) in his study of the rust-flora of the mountainous region of north-central Sweden. He found that a surprisingly large proportion of the rusts of the region were of this kind, amounting in fact to about 39 per cent of the total flora (excluding isolated Uredo, Caeoma and Aecidium forms), while they comprised, according to his estimate, only about 22 per cent in Germany, 20 per cent in Italy, and 13 per cent in Holland.

Data assembled from the North American Flora (Arthur, 1907–27) lends support to these views. In Table 7 (p. 181), the microcyclic

species for all North America are shown to be 18 per cent of the total rust-flora (exclusive of unconnected Uredo and Aecidium), and of these 15 per cent are found in the tropic region, 19 per cent in the temperate, and 23 per cent in the boreal.

In Table 9 the distribution of microcyclic species occurring wholly within the temperate zone is deduced from the local floras of eight states of North America, which can not be said to differ greatly in the monthly succession and range of temperature.

TABLE 9 — LOCAL FLORAS IN THE TEMPERATE AREA OF NORTH AMERICA

	Square Miles	State	Authority	Macrocyclic Species	Microcyclic Species	Total Species*
Mountains	158,360	California....	Blasdale, 1919	191	33, or 15%	237
	96,030	Oregon.....	Jackson, 1918a	173	37, or 21%	220
	84,970	Utah.....	Garrett, 1910–25	152	48, or 31%	223
	69,180	Washington..	Hotson, 1925	169	45, or 27%	224
Plains	36,550	Indiana.....	Jackson, 1916–21	144	17, or 12%	167
	20,550	Nova Scotia..	Fraser, 1913	84	9, or 10%	97
	4,990	Connecticut..	Hunt, 1926	137	12, or 9%	203
	2,050	Delaware.....	Jackson, 1918b	115	9, or 8%	129
		Summary.....	.....	1165	210, or 15%	1297

* As published, including unconnected species belonging to form-genera.

All the areas are distinctly temperate in character. The percentages of microcyclic species to the total flora (exclusive of unconnected forms) however, range from 8 to 31, with an irregularity that at first sight seems unaccountable. By arranging the areas in a series based on the combined annual atmospheric humidity and elevation above sea level they take the following order: (1) Utah, with 31 per cent of microcyclic species, the highest of all, is an arid and mountainous region, cut off from moisture laden winds on all sides; (2) Washington, with 27 per cent, is mountainous and in large part arid, especially the larger eastern portion, although all parts of the state have contributed to the rust-flora; (3) Oregon, with 21 per cent, although directly south of Washington, and partaking of its mountainous and arid character, has supplied few species from its highly arid eastern half, which yet remains largely unexplored for rusts; (4) California, with 15 per cent, stretches north and south through 10 degrees of latitude and from the Sierra Nevada

Mountains westward to the Pacific Ocean, and embraces much mountainous and semi-arid country; (5) Indiana, with 12 per cent, is a fertile region of prairie and forest in the interior of the continent, of moderate elevation and without mountains; (6) Nova Scotia, with 10 per cent, is a maritime province of moderate elevation, surrounded by the waters of the Atlantic Ocean; (7) Connecticut, with 9 per cent, has its southern and longest boundary along salt water and extends inland some sixty miles, with varied topography but not mountainous; (8) Delaware, with 8 per cent, but with a large total rust-flora, is a narrow area along salt water of less than fifty miles in width, slightly above sea level. Although the four areas having the highest percentage of microcyclic rusts are in large part mountainous, while the other four are not, yet the degree of elevation does not in any case cause an average colder climate, in fact they bear the reputation of being somewhat warmer on the whole. Summing up the data for the four mountainous states in Table 9, California, Oregon, Utah and Washington, which have a general elevation above sea level of 4,000 feet or more, they are found to possess 20 per cent of microcyclic species, while the four non-mountainous states, Indiana, Nova Scotia, Connecticut and Delaware, with a general elevation above sea level of less than 1000 feet, possess 9 per cent of microcyclic species.

TABLE 10 — LOCAL FLORAS IN THE TROPIC AREA OF NORTH AMERICA

Square Miles	Country	Authority	Macrocyclic Species	Microcyclic Species	Total Species*	
30,000†	Guatemala	Arthur, 1918b	177	41, or 23%	232	20%
23,000	Costa Rica	Arthur, 1918a	80	28, or 35%	118	
44,000	Cuba.....	Arthur and Johnston, 1918	96	16, or 17%	140	14%
3,600	Porto Rico	Kern and Whetzel, 1926	125	19, or 15%	181	
	Summary..	.....	478	104, or 17%	686	

* As published, including unconnected species belonging to form-genera.
† Exclusive of the Department of Petén, not yet explored.

The above data pertaining to the temperate zone may be compared with similar data from the tropic zone in Table 10, deduced from local floras of Guatemala, Costa Rica, Cuba and Porto Rico, which like those utilized for Table 9 are necessarily of unequal value as to completeness,

but are fairly representative. All four areas are in the same general latitude, but Guatemala and Costa Rica are continental and in large part mountainous, while Cuba and Porto Rico are insular and comparatively low although somewhat mountainous.

The number of species in each area in Table 10 varies directly with the extent of the area, with the exception of Porto Rico. The large representation from Porto Rico is accounted for by the intensive exploration that has been carried on there, and can not be taken as proving a richer rust-flora.

It is a surprise to find that the relation of microcyclic species in Table 10 does not correspond to their relation given for the tropic zone in Table 7, of which the four countries are a part, but approaches more nearly that given for the temperate zone in Table 9. Instead of showing 15 per cent of microcyclic species, as deduced for the tropic zone in general (Table 7), the microcyclic species amount to 17 per cent.

If, however, consideration be given to the topography of the four areas, and the rusts from the elevated lands of Guatemala and Costa Rica be compared with those of the less elevated lands of Cuba and Porto Rico, the microcyclic species will be found to be 20 per cent for the former and 14 per cent for the latter. The latter figure is somewhat greater than for the lower lands of the temperate zone (Table 9), but is accounted for by a greater general elevation.

TABLE 11 — LOCAL FLORAS IN EUROPE

Country	Authority	Macrocyclic Species	Microcyclic Species	Total Species*
Silesia	Schroeter, 1889	136	31, or 19%	202
Finland	Liro, 1908	189	50, or 21%	246
Britain	Grove, 1913b	200	41, or 17%	252
Denmark	Lind, 1913	220	35, or 14%	260
Brandenburg	Klebahn, 1912–14	229	34, or 13%	275
Tirol	Magnus, 1905	229	54, or 19%	305
Bohemia	Bubák, 1908	256	43, or 14%	312
Switzerland	Fischer, 1904	279	75, or 21%	372
Spain	González, 1924–25	334	35, or 10%	433
Italy	Trotter, 1908–14	338	94, or 22%	482
Summary		2410	492, or 17%	2657

* As published, including unconnected species belonging to form-genera.

The data from a number of local floras of Europe are assembled in Table 11. The evaluation of species in these floras is uneven, but the statistics serve a reasonable means for comparison.

Table 11 is arranged in accordance with the numerical abundance both of macrocyclic and total species in the several countries. The microcyclic species, however, show no corresponding uniformity. But by omitting the two southernmost countries, Spain and Italy, which require separate comment, and roughly grouping the remaining countries into the more mountainous ones and the more level ones, a set of data is obtained that corresponds to that secured from the areas of North America displayed in Table 9. The combined data for the more mountainous countries, Finland, Tirol and Switzerland, give 21 per cent of microcyclic species, while the more level countries, Silesia, Britain, Denmark, Brandenburg and Bohemia, give 15 per cent of microcyclic species, which are percentages that correspond with somewhat similar areas in the western hemisphere.

The rust-floras of Spain and Italy have a surprisingly large record of species. This may be due in part to the longer period of time covered and more thorough collections, to the recognition of more biologic forms under the category of species, to the more southern latitude, to the extent of territory covered, to the highly varied topography, or to other causes or a combination of all. The percentage of microcyclic species is also a surprise. Spain has the smallest percentage of the countries listed, and Italy the largest percentage. Assuming that the data are reasonably correct, one might proceed to build theories to explain the seeming anomalies, but as the principal object in recording these statistics is not to undertake a solution of the problem of the origin of microcyclic species but to present one of the features in the distribution of the rusts, no further comment is required.

Leptosporic species. — The prefix lepto[1] came into the terminology of rusts in 1870, when Schroeter proposed the subgeneric division of Leptopuccinia (p. 56). Later, other genera were similarly divided, and eventually such subgenera were occasionally given generic rank. Only microcyclic species were so designated, and only such as showed ready germination when the spores had attained full size. Many species with this characteristic mature the sori consecutively from the center of a group toward the circumference, and as the germination proceeds a cinereous film of basidia and basidiospores is spread over

[1] From the Greek word λεπτος, slender or delicate.

the group. This appearance has come to be the main feature by which the lepto-forms are recognized.

All gradations are known to exist between the true lepto-forms and those which do not germinate until after a period of rest. When both forms are noticeably common in the same species, one is called "forma persistens" and the other "forma fragilipes," as in *Puccinia veronicarum*. It has been shown that even in the most pronounced lepto-forms some of the spores maturing late in the season become resting spores and only germinate at the beginning of the next season for growth (Fischer, 1926b).

A more extensive acquaintance with the rusts has brought species to light that are not microcyclic yet have the same habit of ready germination of the teliospores with the cinereous appearance, both autoecious, *e.g.*, *Uromyces montanus* on Lupinus in Mexico, and heteroecious, *e.g.*, *U. houstonianus* on Sisyrinchium in the eastern United States. It has also been found that many species are capable of ready germination of the teliospores upon maturity without showing a cinereous appearance. Thus the leaf rust of rye, *Puccinia rubigo-vera secalis*, gives germination for a majority of the teliospores upon their maturity, while the similar leaf rust of wheat, *P. rubigo-vera tritici*, gives very slight germination of the teliospores until after a winter's resting period. From this explanation it is evident that the presence or absence of a resting period for teliospores is an adaptive feature entirely comparable to the like condition in seeds of flowering plants, and is without taxonomic significance.

Table 12 — Leptosporic Species in Three Climatic Zones of North America

	Microcyclic Species	Leptosporic Species	Percentage
Canada, Newfoundland and Alaska	51	16	31%
United States and Nova Scotia	126	33	26%
Mexico, Central America and West Indies	75	43	57%
Summary	252	92	37%

The distribution of the microcyclic lepto-forms is especially interesting, as the opinion has been expressed that they are much more common in the warmer regions than northward in colder regions, and in protected valleys than on mountain tops (Dietel, 1902, 1911a; Mayor, 1914). Table 12 takes into account only microcyclic lepto-forms, and uses the

distribution recorded in the Uredinales of North America (Arthur, 1907–27). The data show that more than one-third of all microcyclic species in North America can be classed with the lepto-forms, and that these forms decrease numerically toward the north, but not by a uniform percentage, owing to the great preponderance in the temperate zone of microcyclic species which overwinter the spores.

By taking the local floras used in Tables 9, 10, and 11, and separating the microcyclic lepto-forms, the data in Table 13 are obtained.

The countries that are in general more elevated above sea level and mountainous are contrasted with those that are in general less elevated

Table 13 — Leptosporic Species Recorded in Local Floras

	Countries	Microsporic Species	Leptosporic Species	Percentage	
Mountains	California	35	15	43%	29%
	Oregon	37	12	32%	
	Utah	48	10	21%	
	Washington	45	11	24%	
Plains	Indiana	17	9	53%	45%
	Nova Scotia	9	4	44%	
	Connecticut	12	5	42%	
	Delaware	9	3	33%	
Mountains	Guatemala	41	24	59%	21%
	Costa Rica	28	14	50%	
Plains	Cuba	16	12	75%	69%
	Porto Rico	19	12	63%	
Mountains	Finland	50	19	48%	29%
	Tirol	54	10	19%	
	Switzerland	75	22	29%	
Plains	Britain	41	16	39%	45%
	Denmark	35	18	52%	
	Brandenburg	34	16	47%	
	Silesia	31	15	48%	
	Bohemia	43	17	40%	
	Spain	35	25	71%	
	Italy	94	26	28%	
Summary		808	295	37%	

and broken. It is strikingly shown that the more mountainous regions have a lower percentage of lepto-forms than the more level regions. This relation holds true both for tropic and temperate zones, and for the united countries both in America and Europe without reference to zones. It is also significant that the summary shows more than one-third of the total microcyclic species to be leptosporic, and by coincidence the percentage is identical with that deduced in Table 12 from the total flora of North America.

In explanation of the distribution of leptosporic species Dietel (1911a) has suggested that they are better adapted to moist and warm regions. The data of Tables 12 and 13 give some support to Dietel's views, but make equally clear that neither the distribution nor the origin of lepto-forms can be explained by any single factor of environment, whether it be temperature, moisture, long or short seasons for growth, intensity of light, elevation above sea level, or others not so prominent, but must be sought so far as environment is concerned in some combination of factors.

A most illuminating example, supporting Dietel's views, is that of *Kunkelia nitens*, the microcyclic form of *Gymnoconia interstitialis* on Rubus. In North America the microcyclic form of this conspicuous rust is abundant southward, and intermingles in its northern limits with the corresponding macrocyclic form, which then becomes the prevailing form (Arthur, 1917a). In Europe only the macrocyclic form is known, which does not extend far southward except on mountain tops. It has been predicted that other similarly related species may be found to have a corresponding climatic distribution (Moreau, 1920).

BARRIERS TO DISTRIBUTION

Although our knowledge of the distribution of rusts is imperfect it is obvious, nevertheless, that their spread is restricted by certain natural barriers. These barriers may be due to topography, to climatic or other environmental relations, or to host limitation.

Topographic barriers. — Oceans are the greatest barriers to the distribution of organisms from continent to continent. Even air-borne spores, exceedingly light as they are, can scarcely cross a wide expanse of ocean. Even were this possible, the chances for alighting upon a congenial host and under favorable conditions for growth are so infinitesimally small as to be negligible. Comparatively short distances across areas of water, however, can be bridged. On this basis we may

account in part for the similarity as well as the unlikeness in the rust-floras between the islands of the West Indies, or between the West Indian islands and the mainland of Central America, southern Florida, or northern South America. The large percentage of endemic species in both continental and isolated island areas also indicates a limitation due to expanse of waters. Such limitation does not apply, however, to the arctic region, where the islands and continents may be joined by a continuous solid surface of ice and snow during the winter (p. 169).

Mountain chains are barriers to the free spread of rusts because they interrupt both the continuity of congenial hosts and the favorable meteorologic conditions for infection. The boundaries for many species are marked by the great north and south chains of the Cascade and Sierra Nevada ranges along the western border of North America and extending into the Andes of South America, by the somewhat central Rocky Mountains, and by the Allegheny Mountains near the eastern border of the continent, as well as by the great east and west chains of the Alps in Europe and the Himalayas in Asia.

Deserts, when of sufficient extent, prove a check to the spread of many species, because few species are able to endure extreme arid conditions. Such are the great Gobi and associated deserts of central Asia, the Sahara of northern Africa, and to a lesser degree the arid region between the Sierra Nevada and Rocky Mountains in North America.

Climatic restrictions. — The most important of the limiting factors are moisture, temperature and light. The majority of rusts possess a mesophytic adaptation, that is, they flourish most upon plants which require a moderate supply of water for their development. It is clearly not the percentage of moisture within the host that counts, but the humidity of the air surrounding the plant. A few instances are known of aecia growing normally upon such unlike xerophytic plants as Cactus and Yucca, both inhabiting deserts. The tissues of the Cactus have a very high percentage of moisture, those of the Yucca are low in moisture, but no difference has been noted in susceptibility of the two hosts to rust invasion. On the other hand no rusts develop upon parts of plants continually submerged, but to a limited extent do occur on the upper surface of floating leaves (Limnanthemum, etc).

As a rule desert plants support few species of rusts, which is to be ascribed largely to the lack of moisture on the surface of the plants at the time the spores are in position to germinate and infect the host. Furthermore, the dryness of the air may influence the viability of the spores, even killing them before an opportunity for growth arises.

Basidiospores are especially liable to such injury. With macrocyclic species the atmospheric conditions may limit the full development of the life-cycle without noticeably decreasing the vigor or abundance of the rust. *Puccinia asparagi* in most seasons produces no aecia in midwestern North America, while in the moister regions along the Atlantic and Pacific coasts they occur with normal regularity. An unusually dry season, however, is generally followed by the absence or greatly lessened production of many species of rusts. At the other extreme an excess of atmospheric moisture, as in the tropical rain forests, is equally harmful.

The registration of instruments at a meteorologic station can not be taken as a sure index of the moisture conditions within the plant-cover suitable for germination of spores. In an investigation by Rusakov (1924) the relative humidity among cereal crops was ascertained to be somewhat higher as a rule midway between the plants than above their tops, and this was correlated with a variation in temperature, slightly higher during the day and lower at night. Such a condition of increased humidity among the lower leaves of plants growing close together helps to explain the greater amount of uredinial rust among thickly sown cereals, and such instances as the larger production of aecia of *Puccinia menthae* and some other species on the lowest leaves near the surface of the earth.

Temperature is seemingly a strongly limiting factor both in the latitudinal and altitudinal distribution of rusts. The species in the boreal regions of the north are far less in number and abundance than southward. The data in Table 7 confirm this generally accepted fact, for the number of species in North America is much less in the boreal zone than in the temperate zone, although the two have about the same available area. In fact, not many more than one-fourth as many species are known for the Canadian region as for that of the United States. It would, however, be a hasty conclusion to ascribe this difference in numbers wholly to temperature.

Some species of rusts occur as far north as the shores of the Arctic Ocean. The macrocyclic *Puccinia polygoni-vivipari*, which is also heteroecious, and the microcyclic *P. arenariae*, as well as some other rusts, are not uncommon in the Northwest Territory where the temperature often drops to −35°, or even as low as −48° C. during five months of the year (p. 215). There is no evidence to show that the mycelium, protected as it is by the tissues of the host, is any more liable to injury by cold than the plant within which it grows. But

the propagation of a rust is dependent upon the ability of its spores to germinate and produce infection. All available data (p. 214) indicate that the several kinds of spores may germinate in temperatures which are only slightly above the freezing point, and that the optimum temperature ranges from 12° upward to 23° C. If there are any differences among species in this regard, they will presumably favor the forms naturally growing in cold situations. Indigenous rusts are clearly as well able to perpetuate themselves, so far as temperature is concerned, as the phanerogams which act as their hosts.

As the cold of northern regions restricts the annual period for growth, so it must restrict the number and abundance of species of rusts. This may be partly due to the lessened number of phanerogamic species to act as hosts, but probably more largely due to the restriction placed upon the abundance of spores, an important feature in the maintenance of cryptogamic species.

In one other respect the length of the growing season appears to produce some effect upon the rusts. Not only is the number of species known for the cold zone of North America much less than that for the temperate zone, but the microcyclic species, while reduced to nearly a third, are comparatively more abundant (Table 7). The predominance of microcyclic species may be in part ascribed to the shortened season for growth (Magnus, 1893), or to the excess of spring annuals on which they largely occur and which by their brief period of growth are unsuited to macrocyclic species (Fischer, 1904), or directly to cold, yet these influences must be considered supplementary, and only tending to hasten the general trend toward a shortened life-cycle of the rusts as a whole under all conditions (p. 99).

The factors that change the abundance of species and the length of the cycle in northern latitudes act in essentially the same way for high altitudes (Magnus, 1893).

Another factor in the distribution of the rusts is that of light, although no direct data bearing on its influence can be adduced. Rusts are rare in habitats with deep shade, although moisture, temperature and other factors may be favorable. Such places are deep gorges when overhung with foliage, thick undergrowth in dense forests, the twilight areas in tropical forests, etc. As it seems improbable that this limitation is due to any direct action that light can exert upon the vegetative growth of the rust, we are left to assume that it is shown in the development and maturity of the spores. It may be due to some extent to the amount or intensity of the light in bringing the spores to a state of

viable maturity, or under some conditions to the supply of carbohydrates or other nutriment provided by the plant. The supply of carbohydrates within the host, which is directly dependent upon sunlight, is known to have an effect both upon the kind and quantity of spores produced (pp. 218, 243). Experiments in placing rusted plants in darkness for a time, either at low or room temperatures, have been found to inhibit partly or wholly the production of urediniospores and increase that of teliospores especially with *Uromyces polygoni*, *U. appendiculatus*, *Puccinia antirrhini*, *P. taraxaci*, *P. suaveolens*, and *P. asparagi*, but to a much less extent with *P. rubigo-vera tritici* and *P. sorghi* (Waters, 1928). It may be that through this means the total length of daylight of optimum intensity for the growing season will account in part both for local deviation in spore production and for differences in this regard between the tropic, temperate and boreal areas.

Facility of germination. — Fluctuation in the abundance of a species from season to season is often due to unusual climatic conditions,

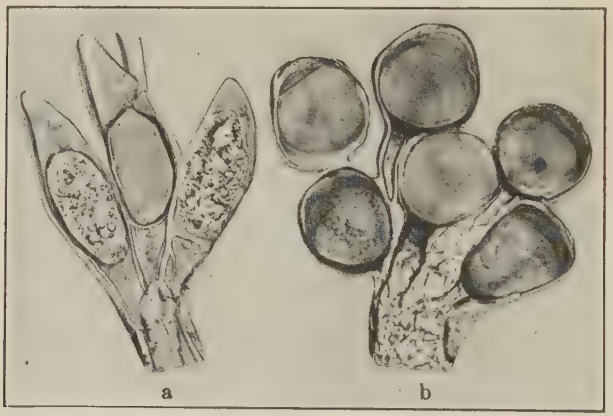


Fig. 124. — Summer and resting spores of the same species: *Uromyces cuspidatus*, *a* summer form, one spore germinating, on Festuca; *b* winter form, on Melica. (After Arthur, 1925; photographs by Holway.)

which may cause the spores to germinate before vegetation is sufficiently advanced to permit infection, or on the other hand may unduly retard germination. The resting spore, which is common among teliospores, and found to some extent among urediniospores (as amphispores), and occasionally among aeciospores, notably in Gymnosporangium, provides a means for the species to tide over unfavorable periods of cold or drought. In some species, *i.e.*, *Puccinia graminis*,

all the teliospores are developed as resting spores, while in others only part of them are so constituted, *e.g.*, *P. rubigo-vera*. Many species among the lepto-forms provide a few spores, especially near the close of the growing season, that are more resistant to unfavorable conditions, and thus continue the species. In the majority of species no conspicuous structural difference is evident to distinguish the spores that possess special resistance.

Some species exhibit a marked difference in form and color between the teliospores that germinate readily and those that do not (Arthur, 1925). The two kinds of spores may be largely in different sori, *e.g.*, the South American *Uromyces cuspidatus* (Fig. 124), or more usually in the same sorus, *e.g.*, *Puccinia interveniens*, abundant in the western part of both North and South America (Fig. 125). Both the examples cited are on grasses belonging to many genera.

FIG. 125. — Summer and resting spores in same sorus; *Puccinia interveniens* on *Nasella chilensis*. (After Arthur, 1925; photograph by Holway.)

The ability to provide both summer and resting spores is a large factor both in extending the range of a species and maintaining it when once established.

LIMITATION DUE TO HOSTS. — The strictly parasitic and highly specialized nature of the rusts precludes their occurrence beyond the limits of the respective hosts. On the contrary the distribution of a given species may or may not coincide with that of its host. *Puccinia punctata* on a dozen or more species of Galium in North America occurs throughout the generic range of the hosts, yet on *Galium aparine* it is found only in western Oregon and Washington, although the host is common throughout the eastern United States, while *P. ambigua* on the same host ranges across the continent on either side of the Canadian boundary, but not southward. *Galium triflorum* is a host for *P. punctata* and also for *Pucciniastrum galii*, but the two rusts appear in north-

western North America and, except for one locality in north-central New York for the latter, not in the eastern part of the continent where the host is abundant. Clearly the presence of a suitable host is not the only factor to determine the general distribution of the rusts.

With the heteroecious species the proximity of the two alternate hosts is not always a necessity, as repeating spores may continue the rust indefinitely in the sporophytic stage, *e.g.*, various species of Coleosporium, which spread to great distances beyond the limits of pines that alone are capable of supporting the gametophytic stage. Other notable examples of the absence of one host without impairing the vigor or limiting the spread of the rust are found among the species inhabiting grasses and sedges, all the cereal rusts, especially *Puccinia rubigo-vera tritici*, being especially prominent in this respect. The presence of uredinia to the exclusion of other spore forms in some species is such a striking phenomenon that many botanists, and among them a few prominent uredinologists, have argued that a stage has been reached in the evolution of such species when the species is incapable of completing its original life-cycle. All known facts, however, are opposed to this view, and go to support the contention that every species will complete its full cycle when suitable conditions are provided.

Macrocyclic rusts without repeating spores, *e.g.*, species of Gymnosporangium, must necessarily be limited in range in each instance to the area occupied in common by the two alternate hosts. This does not imply, however, that the rust will extend as far as the associated hosts are found (Kern, 1911). *G. corniculans* on *Amelanchier canadensis* and similar hosts, and on *Juniperus virginiana* and similar hosts, is a high northern species, while *G. floriforme* on *Crataegus spathulata* and *Juniperus virginiana* is a distinctly southern species.

Distribution between connected and isolated regions. — Regions having similar phenologic characteristics are likely to harbor many of the same or similar species of rusts, and especially if the regions are contiguous. Some rusts of Japan may be found along the southern shore of Alaska and even farther eastward, *e.g.*, *Uromyces miurae* on Fritillaria, which extends as far to the east as central Washington.

The Atlantic and Pacific coasts of North America have species in common that are not found in the interior, as *Uromyces limonii* on Limonium and Statice. Some of the rusts of the Rocky Mountains extend southward along the western part of Mexico, through Central America and along the Andes into South America, as *Puccinia glumarum*, while many species of the great central plains of North America, espe-

cially of the Mississippi valley, extend southward through the West Indies, and into Venezuela and other South American regions, as *P. substriata* on Paspalum and other grasses. Rusts of saline areas occur on the east and west coasts and in the central parts of North America, *e.g.*, *Puccinia subnitens* on Distichlis. The same species may also be found in similar habitats in South America, Asia and Africa.

A discontinuous circumpolar flora has long been recognized both for phanerogams and rusts as shown by *Pucciniastrum arcticum* on Rubus, *Melampsora arctica* on Salix, etc. But more striking because of greater intervening distances is the longitudinal distribution of tropical species. *Uromyces leptodermus* on Panicum is common in the East and West Indies, sub-tropic South America and Japan. *Phakopsora tecta* (*P. commelinae*) on Commelina and Tradescantia occurs in the West Indies, Bolivia, southern Africa, and the Dutch East Indies. *Puccinia kaernbachii* on Andropogon is in Central America, the West Indies and islands of the Indian Archipelago. *Uromyces clignyi* also on Andropogon is in Mexico and the western Sudan, and *U. ignobilis* on Sporobolus is in both the East and West Indies.

Even more striking still is the similarity of the flora of the great plains of North America and the steppes of eastern Russia and southwestern Siberia. *Puccinia universalis* on *Carex stenophylla* with aecia on Artemisia is common to both regions, both as host and parasite. *Puccinia stipae* of the United States and *P. stipina* of Russia are alike, although the aecia are on different groups of hosts. In mountainous regions of both continents are found *Gymnosporangium nelsoni* and *Gallowaya pinicola*, both especially restricted species.

These are some of the more striking examples of a general feature in the distribution of the rusts. As a rule it may be considered possible that the same or similar species of rusts may be found in any part of the world when the same or similar hosts occur and there is a similarity of conditions for growth, as indicated by the seasonal changes in temperature, moisture and light.

Naturally under the limitations enumerated a general zonal distribution may be looked for, ranging from the equator toward either pole. But as there is much less land in the southern hemisphere than in the northern, the likelihood of the presence of the same species in similar zones both north and south of the equator diminishes rapidly upon proceeding toward the poles. In a final analysis the distribution of rusts depends primarily upon the distribution of their hosts.

The existence of many species of rusts, which are local or circum-

scribed in their occurrence, and do not follow any zonal distribution, is probably due to isolated evolution, or to the extinction of intermediate forms. In contradistinction there are also species which may be considered cosmopolitan, and which in one stage at least adapt themselves readily to many kinds of hosts and to many conditions for growth.

Sporadic occurrence of microcyclic species. — It has been a puzzling problem to account for the isolated and infrequent occurrence of certain microcyclic species. The following are given as examples. *Puccinia tolimensis* on Eupatorium has been collected in north-central New York, southern Guatemala and in Colombia in South America, once in each locality. The species is the microcyclic form of *P. eleocharidis*, which has its aecia on Eupatorium and uredinia and telia on Eleocharis, and is common from the Canadian border through the plains and forests of the central United States into the West Indies. *P. polemonii* has been collected once each in north-central California, Idaho and southern Indiana, and also occurs in Norway and Finland. The correlated macrocyclic form has not been identified. *P. ornata* on Rumex has been collected in about eight localities along the northern border of the United States between Maine and Minnesota, once in southern Alberta, and once in eastern Russia. It is correlated with *P. phragmitis* having aecia on Rumex, which is an abundant species on *Phragmites communis* in North and South America, Europe, Africa and Japan. *Puccinia eurotiae* has been collected once in Nevada. It is correlated with *P. burnettii*, having aecia on Eurotia and uredinia and telia on Stipa and Oryzopsis. Both phases of the macrocyclic rust are common in the Rocky Mountains, and the aecia are reported from the Ural Mountains in eastern Russia where uredinia and telia will doubtless be found eventually, and possibly the microcyclic form. Many other examples of a wide and isolated distribution of microcyclic rusts could be cited.

To explain such sporadic occurrence leads us to agree with the theory that microcyclic species are of more recent origin than the macrocyclic (p. 99), that they are derivatives of the latter, and that they may arise at any place or time, and in so doing may become differentiated into distinguishable morphologic forms or races. Some microcyclic species have become so firmly established that they meet all the requirements of independent species, and as such have become widely distributed. They may even have displaced their macrocyclic progenitors. On the other hand an essentially identical microcyclic form may conceivably arise at different localities from a widely distributed macrocyclic species,

or one that was once widely distributed. Such nascent species may fail to become firmly established or to spread with much rapidity. With this point of view there is nothing preposterous in the discovery of the same microcyclic species in limited amount in widely separated localities, even to half the circumference of the earth.

DISTRIBUTION BY GROUPS OF HOSTS

Rusts do not occur upon mosses or on other plants lower than the Pteridophyta. They increase in abundance, but with no apparent regularity, as the hosts ascend the evolutionary scale, the greatest number occurring on the Compositae.

Rusts upon ferns. — Only the ferns (Filices) among the Pteridophyta are known to support rusts, and of these only three families out of the several, *viz.*, Osmundaceae, Schizaeaceae and Polypodiaceae. None of the fern allies, such as Equisetum, Lycopodium, Selaginella and Isoetes, bears rusts. Nearly forty species of fern rusts have been recognized, and of these all except six or seven belong to the genera Uredinopsis, Milesia and Hyalopsora. The other genera are Calidion, with two species known only in the uredinial stage, Desmella with four or five species and one species of Puccinia, all of which are rare. Probably all the species on ferns are heteroecious, but only eight species have yet been cultured, and each of these has aecia on Abies. No correlated microcyclic species are likely to be found on ferns, but they are to be looked for on the coniferous aecial hosts, according to Tranzschel's law (1904).

Rusts upon conifers. — Of the three orders of coniferous hosts rusts occur only upon two, Pinales and Gnetales. All rusts inhabiting conifers are either heteroecious species, or the reduced forms of heteroecious species.

The coniferous hosts may be divided into two groups, (1) the Cupressineae, harboring telia of heteroecious species of the pucciniaceous rusts, and (2) the Pinaceae and Ephedraceae harboring aecia of heteroecious species of melampsoraceous rusts and allied microcyclic species. The alternate hosts in each group belong to a variety of orders and families. Gymnosporangium, representing the Pucciniaceae, is the dominating genus in the first group of hosts. The second group of hosts contains a number of genera of rusts all belonging to the Melampsoraceae, of which Coleosporium and Cronartium have their aecia on hosts usually placed under the genus Pinus, and Pucciniastrum, Melampsora, and a

number of other rust genera have aecia on Larix, Picea, Abies, and related genera.

There are no known microcyclic forms on the first group of coniferous hosts. On the second group of coniferous hosts are the microcyclic species *Gallowaya pinicola* on Pinus, *Chrysomyxa abietis* on Abies, *Necium farlowii* on Tsuga, and two others on Picea.

Rusts upon monocots. — The monocotyledons can not be readily assorted in accordance with the classes of hosts which harbor rusts. Species with various cycles, both microcyclic and macrocyclic, occur in large numbers throughout the group, and belong to both the Melampsoraceae and Pucciniaceae, the preponderance being for the latter.

The two outstanding families among the hosts are the Poaceae and Cyperaceae, which bear a large number of species of rusts, all of which belong to the genera Puccinia and Uromyces. These two families of hosts, sometimes grouped together under the name Glumaceae, bear only telia with their accompanying uredinia, and are consequently heteroecious, with the exception of four imperfectly known species, *Puccinia danthoniae* (McAlpine, 1906), *P. graminella* (Fig. 48), *P. digna*, and *Uromyces pencanus* (Arthur, 1925), all four on grasses. These four species are autoecious and each has its aecia on the same host as the telia, and may be with or without uredinia. There are no microcyclic rusts on the Glumaceae, as indeed, is not to be expected, according to Tranzschel's law (1904) indicating their occurrence (p. 55).

Rusts upon dicots. — Rusts are more numerous upon the dicotyledons than upon the monocotyledons, as could be predicted because of the much larger number both of their genera and species. In general these two great groups of the Angiospermae show no material differences in their relation to the rusts.

The two outstanding families among the dicotyledonous hosts are the Leguminosae (embracing the Mimosaceae, Caesalpiniaceae and Fabaceae) and the Compositae (embracing the Ambrosiaceae, Cardueaceae, and Cichoriaceae). The Leguminosae are notable for harboring all the species of Uromycladium and nearly all of Ravenelia, as well as a large proportion of Uromyces. In North America one-third of all species of Uromyces are on members of this family. The Compositae bear large numbers of rusts, which in many instances are remarkable for their variability and intergradation. In North America the number of rusts on Compositae is about one-fourth of those on all other families combined and on Leguminosae about one-eighth of those on all other families.

The distribution by hosts of some of the largest genera of North American rusts is given in Table 14. The cosmopolitan character of the Uromyces-Puccinia rusts is most conspicuous. All the other genera are highly restricted in their choice of hosts.

Groups of hosts without rusts. — In commenting on the Australian flora McAlpine (1906) remarked that "it is passing strange that upon our numerous eucalypts and kindred species not a single rust-fungus should have developed, while in the Proteaceae, with their wonderful variety of foliage, only a single species, and that a Uredo, is recorded." The list of wide omissions can be much extended. The Typhaceae, simple and presumably primitive monocots, with succulent foliage and growing in marshy places such as are favored by many rusts, yet appear to have nearly or quite escaped attack. No rusts are known upon the large family of palms. Scarcely a species is recorded for the great tropical orders of dicots, the Pittosporaceae with over 100 species, the Epacridaceae with over 200 species, the Dipterocarpaceae with

Table 14 — Rusts of North America by Hosts

(Aecia of heteroecious species are indicated by italics in parentheses.)

		Filices	Conifers	Monocotyledones		Dicotyledones		
				Poaceae and Cyperaceae	Other Families	Leguminosae	Compositae	Other Families
Melampsoraceae	Coleosporium	..	(*16*)	...	...	..	20	10
	Melampsora	..	(*5*)	...	...	..	...	(*4*), 13
	Pucciniastrum	..	(*4*)	...	1	..	...	10
	Cronartium	..	(*6*)	...	...	..	...	6
	Uredinopsis	6	(*6*)	...	...	..	...	...
	Milesia	6	(*2*)	...	...	..	...	...
	Hyalopsora	4	(*1*)	...	...	..	...	...
Pucciniaceae	Puccinia	..	...	142	(*5*), 30	(*1*), 8	(*12*), 115	(*50*), 240
	Uromyces	..	...	33	(*3*), 20	(*1*), 33	(*4*), 14	(*15*), 51
	Ravenelia	..	...	...	...	59	...	1
	Gymnosporangium	..	32	...	...	..	...	(*29*)
	Phragmidium	..	...	...	...	..	...	16
	Uropyxis	..	...	...	...	6	...	4
Summary		16	(*40*), 32	175	(*8*), 51	(*2*), 106	(*16*), 149	(*98*), 351

over 300 species, and the Melastomaceae with over 2700 species. Similarly throughout the plant kingdom we find many species, genera, families, or other groups of vascular plants, which for no reason at present obvious fail to be attacked by rusts.

Parasitic phanerogams without chlorophyll, such as Monotropa, Orobanche and Cuscuta, do not bear rusts, although rusts have been grown on etiolated plants (Mains, 1916) and also on chlorotic plants (Raines, 1922, p. 224; Mains, 1926b). But partial parasites, like Comandra and the Loranthaceae, are equally susceptible with other green plants.

DISTRIBUTION IN TIME

Much side-light could undoubtedly be thrown upon the present geographic distribution of the rust-flora of the world by a study of the geologic record, for which there appear to be data for only a small beginning.

Fossil rusts. — Up to the present time only seven fossil remains have been assigned to the Uredinales. These were found in various parts of Europe, and have been figured with descriptions by Meschinelli (1898). Two of the fossils are considered to be puccinioid telia, and the remaining five to be aecidioid aecia.

The oldest period represented is the Lower Carboniferous, which much antedates the oldest stratigraphic appearance of ferns, which are assumed to bear the most primitive rusts. The collection is that of *Teleutosporites milloti* in the inner cavity of the macrospores of *Lepidodendron esnostensis*. The host is an ancient relative of the lycopods, in a line long since extinct. The drawing represents a single erect spore, which looks somewhat like a spore of *Puccinia graminis*, and yet might equally well belong to other genera of rusts or to other fungi than rusts. Other fungi are figured as arising close by from the same substratum, and all appear from their position more like saprophytes than parasites, one in fact being identified as a Mucor. No instance is known of a rust on any living member of the Lycopodiales. The authors have not seen the original collection, and while it is hazardous to speak without first-hand knowledge, yet there are a number of reasons to believe that this fossil does not belong to the rusts.

The next oldest representative is *Aecidites stellatus* on Dryophyllum, from the Upper Cretaceous, still antedating the appearance of ferns. Dryophyllum is a genus of Fagaceae, and is the supposed stock from which Quercus, Castanea and Fagus were derived. No present-day

aecidioid aecia are known in the family to which these genera belong. The fossil is said to resemble a Rhytisma, and can not be confidently accepted as a rust.

The remaining collections are from the different periods of the Tertiary. *Aecidites nerii* on Nerium, a genus containing the oleanders of the present, is from the Eocene. *Puccinites lanceolatus* on some monocotyledonous host is from the Oligocene. Three collections are from the Miocene: *Phelonites lignitum* on seed of Glyptostrobus, a coniferous genus once common, but now restricted to one species in southeastern China, *Aecidites subcornutus* on Quercus, and *A. rhamni tertiariae* on *Rhamnus rossmässleri*. The remains of the Puccinites are thought to resemble the linear sori of *Puccinia graminis* or *P. arundinacea*, and it would not tax the imagination greatly to consider this form as connected with the Aecidites on Rhamnus, as the latter is said to resemble the present day *Aecidium rhamni*. The Phelonites is considered similar to *Aecidium strobilinum* (*Cronartium flaccidum*), and therefore is the sole representative of the Melampsoraceae among the seven fossils, all the others falling within the Pucciniaceae. The cornute form on Quercus must be wrongly referred, either for its host or for the parasite, but probably the latter, judging from knowledge of living rusts.

Admitting that these seven collections do represent rusts, which is exceedingly doubtful, it would be necessary to assume that the Pucciniaceae had become established in their highest form as early as the Mesozoic and Palaeozoic eras on hosts of a low order not directly represented in the modern flora. It would also be necessary to recognize the full attainment of both melampsoraceous and pucciniaceous forms in the Tertiary, and on present day coniferous and angiospermous hosts.

That only the most modern and best known forms of rusts have been recognized in fossil remains is probably due in large part to the lack of familiarity of those who study the material with the appearance of other genera than Aecidium and Puccinia, and in part to lack of the necessary microscopic technic for demonstrating structure. It is noticeable that no rust has been detected among fossil ferns, although they are the most abundant and best preserved of plant remains. It is further to be noted that only heteroecious species are yet assigned to the fossil record. The study of fossil rusts may some day afford helpful and substantial information, but at present is in need of critical review by a uredinologist familiar with the present state of knowledge regarding rust development.

CHAPTER VI

PHYSIOLOGY

Spore germination: usual procedure; factors involved, water, nutrient solutions, toxic solutions, stimulatory solutions, temperature, oxygen, light, substratum, reserve foods, maturity and dormancy, longevity.

Development of the germ-tube: usual procedure; factors involved, moisture, temperature, light, various solutions; penetration of host, basidiospores, aeciospores, urediniospores.

Infection: definition; first indications, resistance of cell-wall, osmotic pressure, temperature, maturity of host.

Development of the mycelium: extent and duration, source of nutriment, effect of acidity, maturity of host.

Sporulation: specificity; balance between urediniospores and teliospores; relation to supply of nutriment; suppression of spore-stages.

Factors affecting the rust indirectly through the host: mineral nutrients, water, temperature.

Secretions and reserve food: sugary fluid, fragrance, coloring matter, enzymes and toxins.

A consideration of the physiologic processes involved in the development of rusts, as here presented, includes the germination of the spore, growth of the germ-tube, entrance of the germ-tube into the host, establishment of a food relation with the host, development of the mycelium, sporulation and dispersal of the spores.

Studies in the physiology of the rusts are complicated by their obligate parasitism. This condition has made investigation practically impossible during most of the cycle of their development except in connection with the hosts. When studies are attempted in connection with the host the difficulties of technic and the uncertainties of the deductions which can be drawn have discouraged critical physiologic study. The result has been that most of the available knowledge has been accumulated largely in connection with studies in plant pathology, and is scattered through the literature of that subject. A recent résumé and discussion of the relation between parasite and host by Zimmermann (1925) brings together and considers more than 400 citations of literature.

The small portion of the life-cycle which proceeds independently of the host consists of the brief period from spore production until infection. The data obtained during this period from studies of spore germination and germ-tube development afford the most direct and clearest information of the physiologic processes of the rusts.

PROCESS OF SPORE GERMINATION

It is evident that spore germination in all cases must take place through the absorption of water. However, comparatively little is understood about the processes involved. It has been assumed that absorption of water takes place through the cell-wall at any point. If this is the case, the permeability of the cell-wall is an important factor in determining germination in some species and spore-forms which are dependent upon certain changes, such as may be induced by weathering. In many spores, especially those with an indurated wall, there are germ-pores filled with an easily gelatinized substance through which water may readily pass, and which are only covered by the thin cuticle of the spore. However, the question has been raised whether absorption is possible where there is a chitinized cuticle. It has been suggested by Dietel (1915) that in teliospores of this sort water may enter only through the pedicel.

With the intake of water there may be a slight increase in the size of the spore. In any event an increase in turgor must result. With this action the formation of a germ-tube begins, other conditions being favorable. In the basidiospores with thin walls the germ-tube may arise apparently at any part of the spore-wall. While this is also true of the aeciospores, urediniospores and teliospores in some species, yet in most species these spores possess definite places for the emergence of the germ-tube due to modifications of the wall to form germ-pores. These pores are specially noticeable in spores with dark-colored walls, when the modified cell-wall forming the pore is colorless, or only faintly colored. The number and arrangement of pores vary (p. 15). Although several germ-tubes may start from a spore, usually only one continues to develop.

It is not quite clear what relation the germ-tube holds to the spore. De Bary (1887) states that in urediniospores it is the innermost lamella of the endospore which is extruded to form the wall of the germ-tube of urediniospores. Colley (1918) illustrates the germination of an aeciospore of Cronartium (Fig. 82), but expresses no opinion whether the wall of the germ-tube is derived from the wall of the spore or from its plasma. Dietel (1915), however, states that in the germination of the teliospores of *Puccinia malvacearum* (Fig. 28 *A*) the wall of the germ-tube appears not to be a continuation of any membrane of the teliospore. "In the spore-wall of *Puccinia malvacearum*," he says, "three strata are distinct. Of these the outermost, like a cuticle, forms a continuation

of its membrane in a thin layer all around the spore extending to the pedicel. According to de Bary, this is the original, delicate wall of the young spore, which has continued to expand with the growth of the spore. Inside this thin membrane, which forms a club-shaped sack, the two cells of the spore are located, each of which is surrounded by a special membrane, consisting of two strata, a thin interior one and one which fills the space intermediate between the exterior and the interior membrane." Furthermore, he says, "the spore of *P. malvacearum* has no germ-pore, even the innermost membrane does not show one. When the germination begins, the innermost layer of the wall is raised a little, becomes thinner, and is finally resorbed. Furthermore, a part of the intermediate and external layers becomes destroyed and a canal is formed, which is somewhat widened at the surface of the spore. The protoplasm now wanders through this canal in the shape of a naked mass. The delicate wall, which encloses the plasmatic contents of the mature promycelium, is actually formed by this plasma, so that there is no continuation of any of the strata belonging to the wall of the teliospore." In *Uromyces scillarum* there is no pore, but the germ-tube emerges from a slit in the side of the spore (Fig. 126); its wall is a continuation of the endospore (Schneider, 1927).

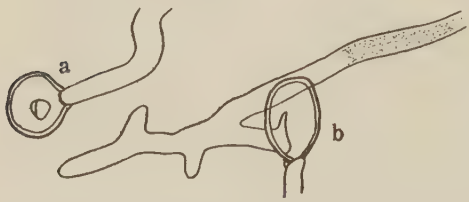


FIG. 126. — Spores of the microcyclic *Uromyces scillarum* in germination: *a* vertical view, showing the germ-tube issuing from the side of the spore, and the hilum at the center; *b* side view, showing the branching germ-tube issuing from a rift in the spore. (After Schneider, 1927; drawing by Ed. Fischer.)

FIG. 127. — Germinating teliospore of *Gymnosporangium globosum* with three germ-tubes from the four pores in each of the two cells. The upper cell shows two basidia, one of which was either an artist's error, or a rare instance of the presence of two nuclei. (After Farlow, 1880.)

The first indication of germination in most cases is the protrusion of a germ-tube. As many germ-tubes may start from a spore as there are pores (Farlow, 1880, see Fig. 127), but except in rare instances where the spore contains more than one nucleus or dikaryon, only one germ-tube from each spore will mature and become efficient.

The protoplasm of the spore with its nucleus and supply of reserve food passes outward with the extension of the tube, water taking its place. The protoplasm continues densely to fill the advancing end of the tube, while it becomes more and more vacuolate toward the posterior part. Probably the protoplasm is withdrawn entirely from the spore and also from the posterior part of the germ-tube as the tube increases in length. With the development of the tube there is a decrease in the reserve food which has served as a source of energy in the process of germination.

The form and function of the germ-tube depend primarily upon the nature of the spore from which it arises, although both may be affected to some extent by environmental influences. With growth from basidiospores, aeciospores and urediniospores, the germ-tube continues as a hyphal tube until a food connection is established with the host, or failing this and its reserve food and energy being exhausted, death results. If a food connection with the host is established, development is continued and a mycelium is produced.

With teliospores, however, there is an entirely different procedure. After the germ-tube has reached a certain growth under normal conditions four cells are produced forming the basidium. Each of these four cells gives rise to a basidiospore, either stalked or sessile (Fig. 29). Thus the germ-tube from the teliospore, unlike that from the other spore-forms, is not an infection-tube but an organ of sporulation.

The germination of rust spores and also the growth of the germ-tube is influenced by a number of different factors, related either to conditions of the spore itself, such as maturity, age, and permeability of the wall, or to external conditions, such as humidity, the presence of various solutes, temperature, oxygen supply, light, and possibly to a slight extent the substratum.

FACTORS INFLUENCING SPORE GERMINATION

Water. — The environmental conditions necessary for spore germination in the rusts are similar to those required in other fungi: water, certain temperatures, and oxygen. Of these the presence of water may be said to be the most essential, for it is by the absorption of water and the resulting increase in volume that the production of a germ-tube is possible. Practically all investigators agree that the humidity necessary for any spore germination whatever must be close to saturation, apparently 95 per cent or higher (Fromme, 1913; Lauritzen, 1919; Melhus, Durrell & Kirby, 1920). Besides high atmospheric humidity

spores of some species apparently must be in contact with water before they will germinate, as Weimer (1917a) found for teliospores of *Gymnosporangium juniperi-virginianae*, Melhus & Durrell (1919) for urediniospores of *Puccinia coronata*, and Hart (1926) for aeciospores and urediniospores of *Melampsora lini*. On the other hand, urediniospores of *Puccinia graminis tritici*, according to Lauritzen (1919), and aeciospores of *Gymnosporangium germinale* (*G. clavipes*), according to Doran (1922), do not require condensed moisture for spore germination. Condensed moisture may, therefore, be chiefly of importance in that it produces in the immediate proximity of the spores, the high humidities necessary for germination. Submersion in water, however, is likely to be detrimental. With urediniospores it either prevents or greatly reduces germination, and with teliospores such treatment results in the promycelium taking on the abnormal form of a long, attenuated germ-tube with irregular septation, or in the production of long sterigmata resembling branches of mycelium, with no basidiospores (p. 292).

Nutrient solutions. — Although the effect of solutions upon spore germination has received considerable attention, yet no substances tried have in general been found to be definitely stimulatory in the sense of serving as food materials for the growth of spores during germination, if an exception be made of the pycniospores. The experiments of Duggar (1901), Ward (1902b), Carleton (1903), Mains (1917), and Hart (1926), indicate little or no benefit to be derived from decoctions of host-tissue, or from decoctions of beets, beans, etc. Various sugars, glycerine, peptone, asparagine, leucine with and without inorganic salts and in various concentrations were not found to have any appreciable benefit (Duggar, 1901; Mains, 1917). Even uncooked water-extracts of fresh host-tissue were not found to possess any stimulatory action and they may even inhibit germination (Reed & Crabill, 1915). In one instance, however, which has recently come to light (Schneider, 1927), germination of the spores of a microcyclic rust, *Uromyces scillarum*, will take place not only in water but much better in a decoction of prunes, horse dung or garden soil. The decoction of horse dung appears to have the most marked effect, both in the rapidity of germination and the production of basidiospores.

On the other hand a sugar solution is apparently necessary for the so-called germination of pycniospores (Cornu, 1876b; Plowright, 1889; Carleton, 1893, 1903; Spaulding, 1922). In such a solution the pycniospores are said to bud like yeasts for a time, and in honey solutions to even form short chains of six or more cells before development ceases,

but unlike the case of yeasts, no alcoholic fermentation occurs (Plowright, *l.c.*). Of the various sugars tried the best results have been obtained with 6 to 10 per cent dextrose (Spaulding, 1922). Usually no indication of germination in pycniospores can be obtained in tap-water, although Carleton (1903) has reported a limited production of germ-tubes.

Toxic solutions. — Many of the inorganic salts are without effect upon germination in such concentrations as do not cause plasmolysis. Thus those of sodium, potassium, magnesium, barium and ammonia, and the salts of nitric, carbonic, hydrochloric, sulphuric, hydrobromic and hydriodic acids, in concentrations as high as 1 per cent, have no action (Wüthrich, 1892; Hitchcock & Carleton, 1893; Stevens, 1898). On the other hand salts of the metals, mercury, copper, iron and zinc, are more or less toxic, and by far the most so is mercuric chloride, with copper sulphate standing second.

The earlier workers generally made their solutions by mass weight, and from such data the effect of mercuric chloride upon urediniospores of *Uromyces caryophyllinus* is to prevent germination in strengths of one part to 1000 (Stuart, 1894, 1895), while with a solution based on molecular weight (method of preparation given by Stevens, 1898, p. 379) germination is prevented in a 6400th normal (Stevens, *l.c.*). Tests made with the urediniospores of *Puccinia graminis* showed no germination in a 1000th normal, or in case of aeciospores in a 10,000th normal (Wüthrich, *l.c.*).

In the use of copper sulphate solutions by mass weight to inhibit germination of urediniospores of *Uromyces caryophyllinus* it requires a strength of 1 : 500 (Stuart, 1894, 1895; Stewart, 1896), while by molecular weight it requires 100th normal (Stevens, 1898; Doran, 1922). Urediniospores of *Puccinia graminis* showed no germination in a solution by mass weight of 1 : 1000 (Carleton, 1893), or a 100th normal for both urediniospores and aeciospores (Wüthrich, *l.c.*).

Recent investigators have used the more exact method of hydrogen-ion concentration, which permits of more accurate comparisons. Of such tests those by Hursh (1922) are especially important in showing the differences in this respect that exist between certain closely related forms and which presumably may be expected to exist between many other such forms and to point to the existence of much greater differences between species.

The solutions employed for the tests were made by mixing one-fifth normal monobasic acid potassium phosphate (KH_2PO_4) with one-fifth

normal hydrochloric acid in order to secure hydrogen-ion concentrations of 2.5 to 4.2, and by substituting sodium hydroxide for the hydrochloric acid to secure a higher range of p_H 5.2 to 8. When used, 50 ccm. of the mixture were diluted with 200 ccm. of water.

Realizing that the degree of toxic action is influenced by many factors, all disturbing conditions except those to be tested were eliminated as far as possible. Two strains of *Puccinia graminis* were selected, one obtained from France and the other from California, both of which had been grown in Minnesota through at least twelve "urediniospore generations" under the same greenhouse conditions. Their physiologic action was studied upon some eleven varieties of wheat belonging to *Triticum vulgare*, *T. durum*, *T. monococcum*, *T. dicoccum*, and *T. compactum*. The Little Club variety of the last species was selected for the tests. On this host both strains grew luxuriantly, while on all but two of the other ten varieties their behavior was very unlike, each variety of wheat being highly susceptible to one strain and almost or quite immune to the other. Three degrees of temperature were used, 10°, 20°, and 30° C. The two strains reacted differently both to temperatures and solutions. In the neutral solution at 20° C., which may be considered about normal for the growth of wheat, with a hydrogen-ion concentration value of p_H 7 the American strain gave 78 per cent germination while the French strain gave 54 per cent germination. The American strain was considerably more tolerant of acidity, at the concentration of p_H 6, giving 94 per cent germination against 84 per cent for the French strain, and at p_H 3.2 giving 32 per cent for the American and 14 per cent for the French, with the limits of acidity for germination nearly reached at a concentration of p_H 2.5. On the other hand the American strain showed less tolerance for alkalinity, giving only 5 per cent germination for a concentration of p_H 8, against 8 per cent for the French strain, this being near the alkaline limits for germination in both instances.

Germination tests with other species of rusts and with other substances, used both dry and in solution, are upon record. Only a few references need be mentioned in this connection. Solutions of potassium sulphide of 1 : 3000 prevent germination of the urediniospores of *Uromyces caryophyllinus* (Stewart, 1896), while much stronger solutions have little or no effect upon the germination of urediniospores of the cereal rusts (Carleton, 1893). Powdered sulphur mixed dry with urediniospores of *Puccinia antirrhini* prevented germination after $3\frac{1}{2}$ hours at room temperature (Doran, 1921). It has been found that "the toxicity of sulphur increases in proportion to the fineness of its particles," and

that it may largely prevent the germination of moist urediniospores of *P. graminis* (Greaney, 1928).

Many organic compounds, such as atropine, aloin, morphine and cocaine, have been found to prevent the germination of urediniospores of *Puccinia graminis* (Carleton, 1893). Potassium cyanide in 100th normal solution can prevent the germination of urediniospores of *Uromyces caryophyllinus* (Stevens, 1898).

A number of workers have noted that when the spores of saprophytic fungi germinate intermixed with rust spores the germination of the latter is often retarded or wholly inhibited. This may be due to the excretion of toxic substances by such fungi, as reported in connection with the spore germination of Botrytis (Brown, 1922), or to other obscure causes. Even tap-water may seriously retard germination (Melhus & Durrell, 1919).

Stimulatory solutions. — The following records show that it is possible in some cases to stimulate the germination of rust spores, although nutrient solutions have been found generally to be inefficient. Weak solutions of hydrogen peroxide hasten the germination of the urediniospores of the cereal rusts (Carleton, 1893; Hitchcock & Carleton, 1893). Ethyl alcohol and sodium chloride will similarly affect the urediniospores of *Uromyces caryophyllinus* (Stevens, 1898); so will vaseline and paraffin oil similarly act upon the urediniospores of *Puccinia coronata* (Melhus & Durrell, 1919) and of *Puccinia helianthi* (Bailey, 1923), although as suggested by Bailey this action may be more physical than chemical. Weakly acid solutions may considerably increase the percentage of germination of urediniospores of *Puccinia graminis* (Hursh, 1922), as recited in the preceding paragraphs.

In some cases stimulation comes from contact with the host. This has been shown to be the case with the aeciospores of *Cronartium ribicola* (Klebahn, 1904a, p. 21). Spores from *Pinus strobus* that gave only slight and tardy germination in slide cultures, produced a vigorous and early infection when placed on leaves of *Ribes aureum*. That the increased growth came from some influence of the host is to some extent indicated by the improved germination that took place when part of the same collection of spores was sown on an agar plate which was made up with a decoction of the Ribes leaves. It has been repeatedly observed by investigators that a test of spores in water culture is not always a sure guide to their power of infection. Although the factors involved have not been investigated, it is quite possible that in some

instances the slight acidity of the moist leaves serves as a perceptible stimulant.

Temperature. — The range of temperature for the germination of spores has been determined by a number of investigators for a score or more of species, but the conditions of maturity, moisture, time since gathering, previous handling, and probably other factors including the luxuriance of development of the fungus from which the spores were taken, have introduced causes for variation in results. In general the range of temperature within which germination takes place is from 1 to 10° up to 25 to 35° C., with an optimum between 12 to 23°. These data are taken from records made by Howell (1890), Gibson (1904), Dietel (1911c), Johnson (1912), Reed & Crabill (1915), Mains (1916), Weimer (1917a), Doran (1919), Lauritzen (1919), Melhus & Durrell (1919), Melhus, Durrell & Kirby (1920), Hoerner (1921), Weber (1922), Bailey (1923), Fukushi (1925), and Hart (1926). The rusts that were utilized are *Puccinia graminis, P. coronata, P. rubigo-vera, P. sorghi, P. antirrhini, P. chrysanthemi, P. helianthi, P. malvacearum, Uromyces caryophyllinus, U. trifolii, Gymnosporangium juniperi-virginianae, G. germinale* (*G. clavipes*), *G. globosum, G. yamadae, Cronartium ribicola, C. comptoniae, C. comandrae, Melampsora larici-capraearum, M. bigelowii,* and *M. lini.* All the records for urediniospores and teliospores agree so closely that no comment is needed, except that both kinds of spores of *P. antirrhini* and also the aeciospores of the other species germinate under somewhat lower temperatures than for the other spores. The aeciospores of *C. ribicola* respond to lower temperatures than do the urediniospores of that species, the aeciospores of *G. germinale* (*G. clavipes*) have a lower optimum and maximum than the teliospores of that species, and the same is true of the basidiospores of *G. juniperi-virginianae* as compared with its teliospores. In contrast, however, the aeciospores of *U. trifolii* do not respond differently than do the urediniospores of that species. The significance of the different response in some instances of aeciospores and basidiospores as compared with urediniospores is not easy to fathom. It may possibly be correlated to the seasonal conditions at the time when these spores naturally appear in the open.

The optimum for the best germination usually ranges over five to seven degrees, although sometimes it may be narrowed to one or two degrees (Doran, 1919). In general the nearer to the optimum temperature the shorter the time that is necessary for germination, at least this is true of urediniospores. Teliospores are not so sensitive, for the

time required for their germination is about the same over a fairly large part of their range of germination.

Under some conditions spores of rusts retain their vitality at temperatures much above and much below those that permit germination. Aeciospores of *Puccinia graminis* have been found to endure −8° to −10° C. for 2 hours and give good germination when tested at favorable temperatures, an exposure of 13 hours being detrimental; urediniospores of the same species may endure −6° C. for 1 hour, those of *P. glumarum* −4.5° to −10° C. for 2 hours, and those of *P. coronata* −10° C. for 2 hours (Eriksson, 1895c). Urediniospores of *P. rubigo-vera bromi* have withstood −5° C. for 10 minutes when frozen in a drop of water, while 4 to 5 hours proved fatal (Ward, 1902b); and teliospores of *Gymnosporangium juniperi-virginianae* exposed over night to a freezing temperature of −6° C. gave 80 per cent germination, while telia of the same species frozen into a block of ice (time not stated) also gave 80 per cent germination of the spores (Reed & Crabill, 1915).

When exposed in the open under natural conditions lower temperatures and longer periods for endurance are indicated. Urediniospores of different strains of two cereal rusts and of *P. poarum* germinated when brought into the laboratory during a winter when the temperature had reached −22° C. (Christman, 1905b), and essentially the same results with urediniospores of three cereal rusts were secured between December and March at St. Paul, Minn. (Freeman & Johnson, 1911). Similar results have also been reported by Hitchcock and Carleton (1893), Bolley and Pritchard (1906), Reed and Holmes (1913), Dosdall (1918), and Weber (1922), the last with urediniospores of *P. sorghi*. Hoerner (1921) claims to have germinated urediniospores of *P. coronata* that had been exposed to −32° C. in a Petri-dish out of doors.

Even lower temperatures than these trials indicate must be endured by the spores of rusts in alpine regions and the far north. *Puccinia arenariae* and *P. polygoni-vivipari* occur north of the arctic circle where the temperature frequently reaches −35° to −48° C. during five months of the year, the average monthly temperature during the time being −19° to −31° C.

There are few records for the upper limits of endurance for rust spores of any kind. The urediniospores of *Puccinia glumarum* when moist will not endure 5 minutes exposure at 45° C. (Butler & Hayman, 1906). The upper limit for urediniospores of *P. rubigo-vera bromi* is given by Ward (1905) as 65 to 70° C., moisture conditions not stated. Teliospores of *Gymnosporangium juniperi-virginianae* give no germina-

tion after being subjected to a temperature of 30° C. for 5 hours (Reed & Crabill, 1915).

Oxygen. — It is a common observation that submerged spores of the rusts germinate poorly and abnormally. This has been attributed to insufficiency of oxygen. It has also been noted (Carleton, 1893; Hitchcock & Carleton, 1893) that urediniospores of several of the cereal rusts germinate better in weak solutions of hydrogen peroxide than in water.

Teliospores and basidiospores of *Gymnosporangium juniperi-virginianae* placed in an atmosphere of carbon dioxide for 5 hours at 18 to 22° C. (Reed & Crabill, 1915) gave no germination, but when restored to outside air 75 per cent of the teliospores and 50 per cent of the basidiospores germinated. Basidiospores of the same rust subjected 24 hours to carbon dioxide when brought into the air under optimum conditions did not germinate. As investigated by Dietel (1921) the teliospores of *Puccinia graminis*, *Melampsora larici-caprearum* and *M. larici-tremulae* when placed in a vacuum for periods varying from 4 to 48 hours showed no germination, but upon exposure again to air germination was obtained. Likewise in an atmosphere of carbon dioxide no germination occurred, while upon again exposing to the air germination was obtained. When air was completely deprived of oxygen no germination occurred. If the oxygen were only partially removed, germination took place. After being completely deprived of oxygen, alternate wetting and drying of the spores was necessary before they were again capable of germination. Similar results have been noted for *Melampsora lini* (Hart, 1926). Dietel comes to the conclusion that oxygen is rather loosely bound within the spores, and becomes partly lost when they are kept in an atmosphere free from oxygen. He also thinks that a sufficient content of oxygen is necessary to render spore-plasma capable of developing basidia.

Light. — The spores of the rusts generally germinate more freely at night, since it is at this time that the most favorable conditions of temperature and moisture are likely to prevail. Darkness, however, is not necessary in order that germination may occur. Given favorable conditions spore germination will take place in the light. With some species, and possibly with most species, whether macrocyclic or microcyclic, more ready germination occurs when teliospores are exposed for several days to the alternating light and darkness of day and night, while continuous darkness for about the same period, either preceding or following the alternating periods, retards germination. This is espe-

cially true of *Puccinia emiliae* on Calendula, *P. xanthii*, *P. helianthi* and *Uromyces caryophyllinus* (Maneval, 1927).

Intense sunlight and light of the blue and ultra-violet end of the spectrum may retard germination or even destroy the viability of spores (Ward, 1902b; Dietel, 1911c; Duff, 1918). In blue light when exposed under conditions favorable for germination, Ward obtained little or no germination of urediniospores of *Puccinia rubigo-vera bromi*, while good germination took place in red and white light. He concludes, however, that with further study it may be found, that even in the case of blue light, the orange-yellow contents of the spores have a protective action. Similar results were also obtained by Dietel, who found that under conditions favorable for germination exposure for 1 hour to blue light delayed germination of the teliospores of *Melampsora larici-capraearum*, as compared with white and red light. Duff states that exposure of urediniospores of *Cronartium ribicola* to glass-filtered sunlight for a few hours at 20° C. increased germination, but that $2\frac{1}{2}$ to $5\frac{1}{2}$ hours at 30 to 44° C. materially reduced the germination. It is likely in the latter case, that temperature was the important factor. Duff also found, however, that when the urediniospores were exposed to light for 45 minutes or 1 hour at a distance of 16 inches from an electric arc, which is rich in ultra-violet rays, the temperature being 20° C., no germination could be obtained. Spaulding (1922) reports that urediniospores of *Cronartium ribicola* taken from bushes of Ribes pulled and hung in the sun ceased germination in 15 days. Urediniospores of *Puccinia coronata* kept indoors in light have been found (Hoerner, 1921) to give germination for only 23 days, as compared with 79 days in darkness.

After 3 hours exposure to sunlight aeciospores of *Cronartium ribicola* as reported by Spaulding (1922) showed a decrease of germination of 50 to 75 per cent, and only one spore in 1500 to 2000 germinated at the end of 8 hours. In the record of studies of the effect of light upon spore germination it is not always clear whether the effect is produced upon the spore itself or whether upon the developing germ-tube, since frequently it is not stated whether the dry spores were employed or those on drops of water and in a humid atmosphere.

Basidiospores are especially sensitive to light; those of *Gymnosporangium juniperi-virginianae* are killed by 2 to 5 hours exposure to direct sunlight (Reed & Crabill, 1915).

Substratum. — It is probable that in general the substratum upon which rust spores may fall is of little importance as far as their germina-

tion is concerned, except in so far as it may be favorable to the retention of moisture. If it furnishes solutes, these may possibly aid in stimulating or preventing germination. When the substratum is the host of the rust, as has already been mentioned, it may possibly stimulate germination. In testing the teliospores of some species at least, attachment to the dead host apparently is of importance. Thus the Tulasne brothers (1847), de Bary (1865) and Melhus, Durrell and Kirby (1920) note a reduction in the germination of the teliospores of *Puccinia graminis* when they are removed from the straw.

As the teliospores of *Puccinia malvacearum* were found to germinate normally only when attached to the rust mycelium in the living host, Dietel (1915) considers that such an attachment is important for their germination, particularly when the surrounding atmosphere is saturated with moisture. He advances the hypothesis that water can enter the teliospore in such cases only through the pedicel. When the atmosphere is saturated with moisture the turgidity of the host is higher, which induces greater turgidity of the rust and in turn the greater turgidity of its teliospores, which results in their germination.

Reserve food. — Without question the conditions which prevail in the host play an important part in determining the vitality of the spores produced. The nourishment of the rust must depend upon the food supply of the host, and this is in turn determined by the effect of various conditions on the metabolism of the latter. When conditions occur which bring about a reduced supply of food, there is probably not only reduction in the number of spores formed, but also in their vitality and in their supply of stored food.

A number of investigators (Carleton, 1893; Eriksson, 1895c; Spaulding, 1922; Mains, 1924a) have noted an apparent connection between the abundance of spores produced and germination, the best germination occurring under conditions which afford great spore production. It appears that in cases of heavy infection with a rapid and profuse sporulation the food producing capacity of the host may be overtaxed and the later formed spores be less capable of germination. Melhus and Durrell (1919), working with urediniospores of *Puccinia coronata* from young plants, found that only 14 per cent of the spores germinated when taken from pustules at the end of 13 days from their first appearance, fewer as the plants declined in vigor, and none at the end of 17 days when the plants died. From longer lived and more mature oat plants on the other hand, with their greater capacity for the production of food, the rust showed 12 per cent germination at the end of 54 days.

It is logical to expect that conditions favoring and hindering photosynthesis, translocation of food, etc., in the host have an important bearing upon spore viability.

Maturity and dormancy. — The maturity of the spores is undoubtedly a determining factor in their ability to germinate. The criteria of full maturity are difficult to specify definitely. If used in the sense of ability to function, germinability would necessarily be the principal criterion, and the teliospores of many species would reach maturity only after overwintering. If used in the sense of being fully formed, the characters of maturity are still harder to define, as they must vary with species and spore-forms, and must depend upon the condition of the spores when at full size, and the color, thickness and markings of the wall, and color of the contents, etc., which may be typical of the particular species. Although generally used in a loose manner, the term, maturity, seems to have been used most in the latter sense of being fully formed, and will be so employed here. In the case of deciduous spores such as the basidiospores, most aeciospores and urediniospores, and some teliospores, they are usually mature when spontaneously detachable.

Very immature spores will not germinate. The spores of some species before they reach full maturity may germinate to some extent. Melhus and Durrell (1919) obtained poor germination of the urediniospores of *Puccinia coronata* the second day after the appearance of the uredinia. Doran (1922) states that urediniospores of *Puccinia antirrhini* will germinate the first day that the uredinia break through the epidermis, but that germination of such spores takes place through a much narrower range of temperature than usual, conditions nearer the optimum being required. Doran also points out that in general the immature spore cannot germinate except under the most favorable conditions for the species and spore-form.

The occasional low germination of urediniospores has been attributed to the presence of immature spores. While this doubtless explains the low per cent of germination in some instances, other factors are usually of more importance.

With the teliospores of many species, and to a less extent with the aeciospores and urediniospores, maturity is not synonymous with germinability. Schaffnit (1909) considers that urediniospores cannot be made to germinate unless they are germinable at the time when they are detached from their pedicels. Melhus and Durrell (1919) found that urediniospores of *Puccinia coronata* showed a decided increase in

germination 5 days after collection. The same result has been noted for the urediniospores of a number of other species.

It has been suggested (Reed & Crabill, 1915) that a period of overwintering may be necessary for the aeciospores of *Gymnosporangium juniperi-virginianae*, and such a condition has been demonstrated for the aeciospores of *G. yamadae* (Fukushi, 1925). It is well known that the teliospores of a number of species have a more or less lengthy period of dormancy before germination can be obtained.

Considerable information is available regarding the factors which are of importance in bringing about a germinable condition. Drying the urediniospores of *Puccinia rubigo-vera bromi* for a short time appears to increase their germination, as also does freezing, probably a similar process physiologically (Ward, 1903a, 1905). Pycniospores, aeciospores and urediniospores of *Cronartium ribicola* have been found to show increased germination when stored for a short time at low temperatures (Duff, 1918; Spaulding, 1922). Similar results have been reported for *Gymnosporangium yamadae* (Fukushi, 1925). Storage of urediniospores of *Puccinia coronata* at 30° C. were found by Melhus and Durrell (1919) to give better germination than at lower temperatures. However, they consider that time is of more importance in this connection than temperature.

The low germination obtained sometimes under apparently optimum conditions (Melhus & Durrell, 1919; Mains, 1924a) is too low to be ascribed entirely to immature spores, and increase in germination may be due to a condition of dormancy in some of the spores, requiring a period of after-ripening or some stimulation before becoming germinable, a situation probably similar to that found in many seeds. That a modified type of urediniospore, the amphispore (p. 16), which is found in such species as *Puccinia vexans*, *P. scaber*, *P. caricis-strictae* and *P. atro-fusca*, goes through a period of dormancy is known. This type of spore germinates like a urediniospore, but it possesses various modifications, being thick-walled with colorless contents, and germinating only after overwintering (Carleton, 1904). This probably represents the most extreme type of dormant urediniospore.

While the possibility of dormancy in aeciospores and urediniospores has not been given much consideration, it is a well recognized situation in the teliospores of many species. In this type of spore the period of dormancy serves to prevent the development of a germinable condition until after winter has passed and favorable conditions for the development both of host and rust again occur. This dormancy can, however,

be terminated by certain treatment long before the spores naturally attain the germinable condition. Thus Klebahn (1914) for *Puccinia graminis*, *P. phragmitis* and *P. magnusiana*, Mains (1916) for *P. sorghi*, Dietel (1921) for *Melampsora larici-capraearum*, and Maneval (1922, 1927) for *Puccinia asparagi*, *P. helianthi*, *P. menthae*, *P. fraxinata* (*P. peridermiospora*), *P. ruelliae*, *P. sorghi*, *P. verbenicola* (*P. sydowiana*), *P. windsoriae* and *Frommea obtusa* (*Phragmidium potentillae-canadensis*) found that teliospores may be made germinable, either by alternate wetting and drying or by continuously floating on water, in a much shorter time than the winter period. Treating with citric acid has been said to bring about a germinable condition in *Puccinia graminis tritici* (Thiel & Weiss, 1920), but not in *P. helianthi* (Bailey, 1923). The period of dormancy for the teliospores of *Melampsora lini* was not shortened when subjected to various treatments (Hart, 1926). Conditions may occur in the field during the fall of the year to bring about a germinable condition in teliospores of species in which this condition is not usually found until spring (Mains, 1924a; Mains & Jackson, 1924).

The factors involved have not been definitely determined, and it is likely that dormancy in the different spore-forms of different species may be due to different causes. Aging or aftermaturing of the protoplasm is not apparently an important factor in the case of teliospores, although it may play some part. Maneval (1922) reports that teliospores of *Puccinia helianthi*, collected in October and kept dry in the laboratory until April, required only 38 days of soaking before becoming germinable, while another collection of the same rust, taken in October and at once placed to soak, required 70 days before any germination occurred and 103 days before germination was good. Apparently, however, storing teliospores dry even for periods equivalent to the period of overwintering does not necessarily render them germinable. Thus McAlpine (1906) found that teliospores of *Puccinia graminis* kept over winter at 4° and −18° C. indoors gave no germination while those exposed outside did. In consequence, it would appear that other factors besides aftermaturity are of importance in the case of teliospores.

It is likely that permeability of the cell-wall to water plays an important part in relation to dormancy, and in addition the entrance of oxygen may also be of importance as indicated by the results of Klebahn (1914), who was able to induce germination by soaking, when the water was frequently changed. As a result of their investigations Thiel and Weiss (1920) are inclined to doubt that the effect of moisture upon dormancy is wholly determined by the cell-wall.

Longevity. — The longevity of spores depends upon a number of factors, such as light, temperature, and moisture, and also on the species of rust, and the kind of spore. The basidiospore has the shortest period of viability, as might be expected from its nature. Basidiospores of *Cronartium ribicola* may be killed by an exposure of 10 minutes at a humidity of 90 per cent and a temperature of 19° C. (Spaulding, 1922). Basidiospores of *Puccinia malvacearum* have been found (Dietel, 1915) to remain viable from 4 to $4\frac{1}{2}$ hours at 96 per cent humidity, 1 hour at 92 per cent, but were killed in 1 hour at 90 per cent. Abundant infection was obtained after 1 hour at a humidity of 98 to 99 per cent, but none was obtained after 10 and 16 hours at 100 per cent. Basidiospores of *Gymnosporangium juniperi-virginianae* have been found (Reed & Crabill, 1915) to remain viable 3 days in the laboratory at 15 to 21° C., but were killed in less than 12 hours when kept in dry air over calcium chloride. It is evident that basidiospores are very sensitive to drying, high humidities being necessary for retention of viability. Even under optimum conditions they have very short periods of viability when compared with other kinds of rust spores. This is likely due to their thin walls.

Pycniospores, judging by their appearance, may react in a similar way to basidiospores. Spaulding (1922), however, states that the pycniospores of *Cronartium ribicola* were kept viable for 18 days when stored in a refrigerator.

Some attention has been given to the longevity of aeciospores, especially those of *Cronartium ribicola*. Observations with this species indicate that viability may be retained for considerable periods under favorable conditions. Klebahn (1904a) found that they remained viable for 35 days. Spaulding (1922) cites observations made under a variety of conditions by a number of investigators. Spores from unopened aecia on leaves stored in a bag in the laboratory retained their viability for 157 days, while in the open, although protected from sun and rain, the period was shortened to 75 days. Dosdall (1918) obtained infection from aeciospores of *Cronartium ribicola* that had remained in the open throughout the winter.

The aeciospores of *Gymnosporangium globosum* have been found to germinate for a period of 80 days (Weimer, 1917a). Leaves of apple infected with *G. yamadae*, gathered August 8, placed in a cotton bag and left in the open tied to the branch of a small tree, supplied aeciospores that germinated vigorously 212 days afterward. The next season under similar conditions the period was only 177 days. While this species

gave much better germination of the aeciospores after overwintering, those of *G. haraeanum* on the contrary germinated best immediately upon maturity (Fukushi, 1925).

The aeciospores of *Cronartium melampyrum* (*Peridermium sorraueri*) remained viable for 20 days (Klebahn, 1904a). For the aeciospores of *Puccinia helianthi* a humidity of 80 per cent was found by Bailey (1923) to be most conducive to longevity, the humidity being of more importance than temperature. However, he found that only about 5 per cent germinated at the end of 56 days, a period much shorter than for urediniospores of the same species.

More information is available concerning the longevity of urediniospores. The following are typical of the results obtained. Thus it has been found that urediniospores of *Puccinia graminis* remained viable for 365 days (Peltier, 1925), *P. glumarum* for 63 days (Hungerford, 1923), *P. coronata* for 87 days (Hoerner, 1921), or even 164 days (Maneval, 1924), *P. himalensis* for 135 days (Barclay, 1891), *P. rubigo-vera tritici* for 235 days (Ducomet, 1925), *P. sorghi* for 180 days, *P. prenanthis* for 220 days and *P. bupleuri* for 356 days (Barclay, *l.c.*), *P. menthae* for 173 days and *Uromyces caryophyllinus* for 185 days (Maneval, *l.c.*), *U. pisi* and *Melampsora lini*, each 75 days (Barclay, *l.c.*), *M. lini* for 77 days (Hart, 1926), *Cronartium ribicola* for 80 days (Spaulding, 1922), and *Phragmidium rosae-alpinae* for 82 days (Gibson, 1904). Exposure to sunlight shortens the period of viability (p. 217).

Peltier (1923) found that urediniospores of *Puccinia graminis tritici* "III" retained their viability best at a moderate humidity, while the period of longevity decreased considerably both at greater and lesser humidities. At each percentage of humidity the longevity was greater at the lower temperatures, showing a reciprocal action between humidity and temperature. The table on the next page is taken from Peltier.

Humidities of 20 to 40 per cent were found by Bailey (1923) to be the optimum for urediniospores of *Puccinia helianthi*, and at temperatures up to 23° C. they retained their viability for at least 185 days. For *Melampsora lini* a temperature of 7° C. and a relative humidity of 40 per cent is the most favorable to longevity (Hart, 1926).

Teliospores of many species, of course, remain viable for a number of months, since in cold regions they function as resting spores to carry such species through the winter and in arid regions through the dry period.

Of those species, in which the teliospores remain dormant over winter, *Puccinia graminis* is the only one for which data appear to be available.

TABLE 15 — THE NUMBER OF WEEKS THAT THE UREDINIOSPORES OF *Puccinia graminis tritici* "FORM III" WERE CAPABLE OF PRODUCING INFECTION AFTER BEING EXPOSED TO VARIOUS TEMPERATURES AND RELATIVE HUMIDITIES.

Percentage of Relative Humidity	25° C.	20° C.	15° C.	10° C.	5° C.
100.0	0	1	0	1	0
89.9	0	0	0	0	1
80.5	0	1	1	2	2
70.4	0	1	2	16*	16*
60.7	2	0	14	14	16*
49.0	2	1	15	16*	16*
38.0	0	1	14	14	15
29.5	0	1	1	3	4
21.5	0	0	1	2	4
10.5	0	0	1	0	0
0.0	0	1	1	5	0

* Experiment was discontinued at the end of 16 weeks on account of lack of material.

In such species we have the situation of spores being viable but not germinable for varying periods of time, especially during the winter or the arid months. The natural process of bringing such spores out of their dormancy into a germinable condition is through weathering conditions. The apparent longevity of teliospores may thus depend on whether they are dormant or whether they have naturally or artificially been brought into a germinable condition. Eriksson (1897b) investigated these points for *Puccinia graminis*. He found that germination was obtained in several instances when teliospores were kept dry in the laboratory for 1 year and then overwintered, "a total of 18 months." In one instance teliospores kept dry in the laboratory 2 years and then overwintered (a total of 36 months) gave germination. On the other hand if teliospores were overwintered the year they were formed and then brought into the laboratory the next April, they retained their viability for only 122 to 159 days. Melhus, Durrell and Kirby (1920) found that teliospores of this species under similar treatment ceased germination in less than 82 days. It appears, that once out of their dormancy and in a germinable condition, teliospores do not retain their viability any longer than aeciospores or urediniospores.

Of those species in which the spores germinate at once, *Cronartium ribicola* apparently is the only one for which there are data. Spaulding

(1922) reports that teliospores of this rust may retain their viability for 90 days, when kept in darkness in the laboratory.

Summary for longevity. — From the data at hand it appears that longevity of the various kinds of spores is favored by moderate humidity (saturation in the exceptional case of basidiospores), low temperatures (5 to 15° C.), and darkness, or at least absence of direct sunlight. An important factor appears to be the condition of the spores as affected by vigor of the mycelium from which they were produced, which in turn was determined by the food supply available from the host. Poorly nourished spores lose their viability in a comparatively short time. Even in well developed and similar spores there are differences, some rapidly losing their viability, a few retaining it. Doran (1922) states that for aeciospores of *Cronartium ribicola* there is a sharp decrease during the first few days in the percentage of spores germinating, amounting to 71 per cent in 3 days, after which there is only a gradual reduction for a comparatively long time. At such times the surviving spores become greatly reduced in vigor, and the conditions under which they germinate gradually become narrowed toward the optimum for the species. Weber (1922) has also found that for some spores the time for germination lengthens. Inoculation with spores whose germination is long delayed gives a weak infection, according to the results obtained by Eriksson (1897b) with two-year-old teliospores of *Puccinia graminis tritici*.

FACTORS INFLUENCING THE DEVELOPMENT OF THE GERM-TUBE

In the development of germ-tubes, as has already been pointed out, there is a sharp differentiation into two types, those from the teliospores developing into a sporulating organ, the basidium, those from aeciospores, urediniospores and basidiospores developing into an infection tube. As one would naturally suppose, the physiologic responses of the two types are different, and they will be discussed separately.

Germ-tubes from teliospores. — When a teliospore germinates (except in Coleosporium and a few other genera), it pushes out a germ-tube which under favorable conditions is relatively short. Four (rarely two) cells are then formed, each with a short projection, or sterigma, bearing a basidiospore.

The most important factor for the normal development of the teliosporic germ-tube is that of humidity. A nearly saturated atmosphere, 95.6 per cent according to Melhus, Durrell and Kirby (1920), is necessary for its proper formation. Just how much variation of the humidity

or duration of time it can withstand when formed is not known. It is improbable that the exposure can be long. The germ-tube does not usually develop normally when entirely submerged, and according to Melhus, Durrell and Kirby (1920) the same is true of the germ-tubes of *Puccinia graminis* in a saturated atmosphere. This behavior is usually ascribed to a deficiency of oxygen. In the case of *P. malvacearum* normal germination will take place under water, if the water be aërated (Doran, 1922).

Apparently the teliosporic germ-tubes are negatively hydrotropic. This causes them to grow outward away from the wet teliospore-mass and brings the basidiospore into a more favorable position for dispersal. According to Dietel (1912a) there is no geotropic response, the germ-tubes growing either upward or downward from the moist substratum, depending upon the position of the teliospores.

Temperature has a marked influence upon the development of the germ-tube. While the teliospores may germinate at temperatures up to 30° C., in a number of species 23 to 26° C. prevents proper formation of basidiospores. Dietel (1912a) states that the development of the germ-tubes of *Puccinia graminis* proceeds normally up to 22° C. At 23° C., however, the germ-tubes are thicker, spirally twisted at the ends, and while divided into cells do not develop sterigmata or basidiospores. After having germinated at the higher temperatures lowering of the temperature may result in the development of a few long sterigmata but not of basidiospores.

Insufficient turgor, resulting in an abnormal germination and oïdium-like formation, may be brought about by wilting or drying of the host in such species as *Puccinia annularis* and *P. malvacearum* (Dietel, 1912a).

Germ-tubes from aeciospores and urediniospores. — In the germination of aeciospores and urediniospores the germ-tubes rarely become septate before entrance into a favorable host and the establishment of a food connection. The germ-tubes grow with considerable rapidity, often attaining in an hour lengths equaling two to five times the diameter of the spore. In some species the tubes are fairly straight or but slightly curved, in others variously twisted or distorted, in others many short side branches are formed (Fig. 41). Growth takes place at the expense of reserve foods, and when these are exhausted, if the germ-tube has not infected a favorable host, it soon dies. Since the presence of such a host is not a necessary condition for germination, any moist substratum sufficing, there must be a high mortality among the spores.

Moisture plays an important part in the development of germ-tubes,

and yet they will withstand drying, if not too prolonged (Doran, 1922). In some instances germ-tubes of this type show a hydrotropic response. Unlike the germ-tubes of teliospores, they give a positively hydrotropic reaction. Balls (1905), using rubber membranes pierced with holes the size of stomata, found that the germ-tubes from spores on the surface turned and passed through these openings into the moister atmosphere beneath. Ward (1902b) explains that the poor infection which he obtained, when wet cotton-wool was placed on the leaves of the host, was due to the germ-tubes growing into the damp interspaces of the cotton-wool, rather than into the host.

Temperature is another factor that has a marked effect upon the development of germ-tubes of aeciospores and urediniospores, and probably a similar effect upon those of basidiospores. The data available indicate that those temperatures that are optimum for the initiation of germination are also optimum for growth of germ-tubes. Melhus and Durrell (1919) however, found that the response to temperature was greater for the germ-tubes, as indicated by the amount of growth, than for the spores, as indicated by the rapidity of germination. They record the following average growth (time not stated) for the germ-tubes of urediniospores of *Puccinia coronata* at different temperatures: 1° C., 0μ; 5° C., 52μ; 8° C., 296μ; 13° C., 468μ; 17° C., 588μ; 20° C., 687μ; 25° C., 504μ; 30° C., 180μ; 35° C., 7μ. At the higher temperatures the germ-tubes become decidedly vacuolate and show evidences of injury.

In some few species, light has been shown to cause a very definite reaction in the growth of the germ-tube. While light of certain wave lengths is detrimental, it is uncertain from the data at hand, whether the results noted are due to action on the germ-tube or on the spore.

In certain species germ-tubes have been found to show a decided phototropic (heliotropic) response. Thus Fromme (1915) and Mains (1916) for urediniospores of *P. coronata* (Fig. 128), and Dodge (1923a) for aeciospores of *Gymnoconia interstitialis*, note a negative phototropic response, yet in a number of other species, the germ-tubes apparently are not influenced by differences in the incidence of light.

In connection with the study of the effect of various solutes on germination some mention has been made of the effect upon germ-tubes. The action depends not only upon the nature of the solute, but also on its concentration. In the case of toxic substances, at concentration too weak to prevent germination, the germ-tubes produced may be

stunted, knotted and otherwise distorted and the protoplasm may show injurious effects by its granular, extremely vacuolate condition. Stevens (1898), however, makes the observation that an occasional germ-tube from a urediniospore of *Uromyces caryophyllinus* may develop more or less normally in solutions which prevent the germination of most of the spores.

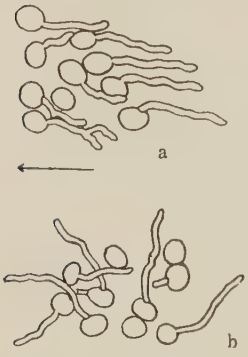


FIG. 128. — Phototropic response of germinating urediniospores of *Puccinia coronata: a* grown with illumination from one side, arrow shows the direction of light; *b* grown in darkness. (After Fromme, 1915.)

From the data at hand it is uncertain whether germ-tubes react chemotropically or not. Miyoshi (1894) states that decoctions of wheat leaves bring about a positive chemotropic response for germ-tubes of *Uredo linearis* (*Puccinia graminis?*). The germ-tubes of both aeciospores and urediniospores may enter the stomata of many unrelated plants, as has long been known. It has been pointed out (Gibson, 1904) that, if a chemotropic response is an important factor in inoculation, the substance responsible must be found quite generally in plants.

GERM-TUBES FROM BASIDIOSPORES. — Basidiospores are very small and the amount of available nutriment they contain does not permit of much growth before exhaustion results or entrance has been made into the host. If the basidiospore is attached to the host under favorable conditions for growth a fine point punctures the cuticle and expands in the cell beneath and soon forms hyphae. Except in mode of entering the host, basidiospores react to external agents much like aeciospores and urediniospores. A phototropic (heliotropic) response is shown by the germ-tubes from the basidiospores of *Puccinia malvacearum* (Robinson, 1914), by turning away from the source of light (Fig. 129).

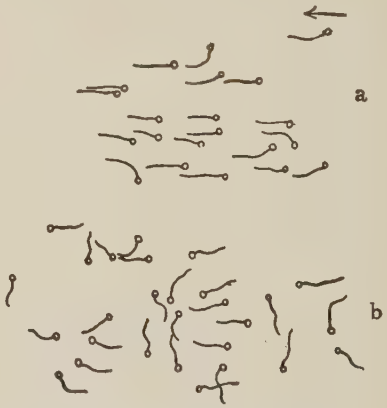


FIG. 129. — Phototropic response of germinating basidiospores of *Puccinia malvacearum: a* grown with illumination from one side, arrow shows the direction of light; *b* grown in darkness. (After Robinson, 1914.)

When basidiospores are submerged in a drop of water the germ-tubes grow very long and in the direction of free air (Fig. 130). When growing on gelatine in a saturated atmosphere, however, the germ-tubes may penetrate the gelatine (Robinson, 1914). Both instances correspond to conditions usually present when basidiospores germinate in a film of moisture on the surface of a host.

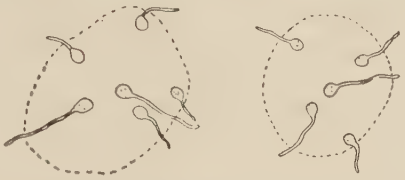


Fig. 130. — Basidiospores of *Puccinia malvacearum* submerged in drops of water: all germ-tubes have grown out of the water into the saturated atmosphere of the glass slide. (After Robinson, 1914.)

Penetration of the host. — The method by which the germ-tube gains entrance into the host, in many species at least, depends upon the type of spore from which it has arisen. The entry of the germ-tubes of basidiospores and those of aeciospores and urediniospores is usually by two quite distinct methods, and they will therefore be considered separately.

De Bary (1865, 1887) figures the penetration of the germ-tubes of basidiospores of *Puccinia graminis*, *Uromyces fabae* (Fig. 30) and *Endophyllum euphorbiae* directly through the upper wall of the epidermal cells of their hosts. He shows that the same occurs for *Puccinia straminis* (*P. rubigo-vera secalis*) in entering the epidermal cells of *Anchusa arvensis*, and further states that the same occurs for *P. coronata* and *Endophyllum sempervivi*. Other observers have noted similar penetration in other species (Reess, 1865; Klebahn, 1896; Fischer, 1901).

De Bary (1887) suggested that the germ-tubes of basidiospores split the epidermis by mechanical means. Waterhouse (1921) has studied the process in *P. graminis* and reaches the conclusion that the germ-tube penetrates the epidermal wall solely by mechanical force. He finds that the germ-tube has a mucilaginous covering which firmly fastens it to the epidermis. An appressorium may or may not be formed. A very fine beak is developed from the end of the germ-tube, or less often directly from the basidiospore. This beak punctures the cuticle and the underlying cellulose layers of the wall of the epidermal cell (Fig. 131), and then swells into a vesicle inside the cell. The further development has not apparently been completely traced.

In some species germ-tubes from the basidiospores may enter quite regularly through the stomata. De Bary (1863a) has noted this for *Puccinia arenariae* (*P. dianthi*) and it may be true of some other species. The process by which germ-tubes of urediniospores enter a host

has been described in detail, for *Puccinia rubigo-vera bromi* (Ward, 1903a; Evans, 1907), *P. graminis phlei-pratensis, P. anomala* (*P. simplex*) and *P. sorghi* (Evans, 1907), *P. coronata* (Evans, 1907; Ruttle & Fraser, 1927), *P. graminis tritici* (Stakman, 1915; Allen, 1923a), *P. rubigo-vera tritici* (Allen, 1926b), *P. glumarum* (Marryat, 1907; Evans, 1907; Allen, 1928) and *Cronartium ribicola* (Clinton & McCormick, 1919). While the process varies somewhat with different species, it is similar in many of its details. The developing germ-tube adheres closely to the epidermis. It may form various swellings, especially in the furrows of the leaf or at the base of hair-cells. When a stoma is reached in some species, especially in some of the cereal rusts, a very pronounced swelling, the appressorium, is formed, into which the protoplasm flows. From the appressorium a narrow extension passes through the stomatal slit into the intercellular space below, where it again enlarges to form the substomatal vesicle (Fig. 115). As the protoplasm passes into this vesicle, the germ-tube and appressorium dry up. The shape of the substomatal vesicle may vary somewhat with different species of rusts, but generally it has its long axis parallel to the stomatal slit.

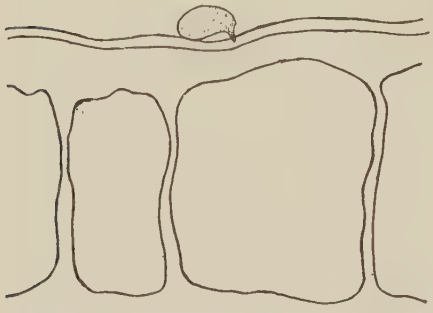


FIG. 131. — Basidiospore of *Puccinia graminis* puncturing the cuticle of a leaf of Berberis; the mechanical pressure required has lifted the front part of the spore from the surface of the leaf, while the rear part is still adhesively attached. (After Waterhouse, 1921.)

The number of hyphae arising from the substomatal vesicle apparently depends upon the species of rust. In some species only one hypha forms, usually from one end. In other species two or more hyphae may grow out, all but one often becoming abortive. With the development of the hyphae the substomatal vesicle sometimes becomes divided by one or more septa, or it collapses and disappears, depending upon the species.

The developing hyphae are closely applied to the lower side of the epidermal cells, or occasionally grow directly across the intercellular space. Eventually a haustorium is formed, which penetrates into the host-cell, and terminates the independent existence of the rust. The success or failure to establish a food connection with a host-cell by

means of the haustorium determines whether or not a mycelium can be developed.

Observations on the development of germ-tubes both of urediniospores and aeciospores, when they enter plants other than their hosts, show that the type of entry through the stoma is normal, yet the stage of development is variable (Gibson, 1904). Sometimes the germ-tube does not progress farther than a swelling in the stomatal opening. At other times it may form a substomatal vesicle, from which hyphae may or may not develop. The extent to which these hyphae grow also varies. Some develop until they reach a host-cell, where the tip swells up, but there are usually no indications of the formation of haustoria. Generally at the end of four days the capacity for growth is exhausted, and even in two days many hyphae are dead. While this condition is possibly brought about by starvation, there is some evidence that substances poisonous to the rust may be emitted by the host-cells.

INFECTION

Definition. — The entry of the germ-tubes of urediniospores and aeciospores, and in some cases basidiospores, through the stomata into the substomatal cavity is not infection. The entire development up to the point at which a haustorium enters the host-cell is entirely a process carried on at the expense of the reserve foods of the spore. Ward (1905) emphasizes this view. He states that the entrance of the haustorium into a host-cell is to be considered the first act of infection. To the preliminary process of entrance and substomatal development he applies the terms "entry or inoculation." "Inoculation" is, however, an unfortunate term to use, since it is in general use for the act of exposure to a pathogen. Peltier (1923) uses the term "period of initial infection." This, however, implies subsequent infection, and it has been shown (Gibson, 1904) that initial entry is no index of the capacity of the germ-tube to infect a plant.

It seems more in keeping with pathogens in other groups of fungi to consider infection as occurring when the rust first affects the metabolism of its host. The physical manifestation of this is usually the penetration and development of haustoria in host-cells. The observations of Allen (1923b), however, indicate that in certain highly resistant hosts, before death results, a rust may develop haustoria to some extent without apparently deriving food from the cells.

Susceptible hosts. — The process of infection has been worked out in considerable detail by Ward (1903a), Evans (1907), Marryat (1907), Stakman (1915) and especially Allen (1923a, b) and Ruttle and Fraser (1927). In susceptible hosts it generally occurs as follows: when a hypha proceeding from the substomatal vesicle runs squarely against a host-cell its growth is halted. The tip of the hypha then swells up and becomes closely applied to the wall of the host-cell. A septum now forms, cutting off this terminal swollen portion, which becomes the mother-cell of the haustorium. Just exactly what occurs immediately following is uncertain. It may be that penetration into the host-cell takes place by puncturing with a fine tube as Waterhouse (1921) finds for basidiospore infection, or possibly enzymatic action effects a small opening. Allen (1923a, b) is inclined to favor the latter method, a fine ultramicroscopic pore being formed through both the fungal and host-cell wall, through which the protoplasm of the rust penetrates. After entry into the cell the protoplasm of the rust apparently pushes the host's protoplasm ahead of it, causing an invagination of the protoplast without breaking the plasma membrane. The haustorium continues to enlarge, receiving most of the protoplasm from the mother-cell. By means of the haustorium the rust begins to obtain food from the host, and without pronounced injury to the latter. With the food derived from its host the rust is able to develop a mycelium. A branch is pushed out from the hypha, back of the mother-cell of the haustorium, which produces another haustorium in another cell of the host, and so on.

Apparently in susceptible hosts a very delicate balance is established between the rust and the host-cell. The protoplast of the host shows no signs of attack, and for some time little disturbance is evident. With the development of the mycelium the older infected cells usually show (Allen, 1923b) an increase in the size of the nuclei (Fig. 171), possibly correlated with the increased drain on its food resources and as a consequence the speeding up of its metabolism. The enlargement is followed by the collapse of the nuclei. During severe infection the heavy drain on the food supply results first in yellowing and later in the death of the infected part, including the mycelium of the rust. With slight infection or where considerable reserve food is available there are few or no detrimental results apparent for some time.

Resistant hosts. — In resistant hosts a balance is not established between the rust and the host-cell, and often a decidedly antagonistic reaction occurs (Marryat, 1907; Stakman, 1915; Allen,

1923a, b; Ruttle & Fraser, 1927). The germ-tube may develop in resistant hosts in a more or less normal way up to the point where the formation of haustoria occurs. When entering the stoma of a species other than its host, the germ-tube may die shortly after entrance (Gibson, 1904). However, with the initiation of haustoria, quite a different reaction takes place in resistant varieties than occurs in susceptible varieties, even of the same species. Sometimes when the protoplasm of the haustorium of the rust and of the host-cell come into apparent contact there results a shrinkage and collapse of the protoplasm of the haustorium. At the same time there is apparently an increase in turgor of the host-cell, rapidly followed by a collapse of this cell also. Apparently the contact of the protoplasts of the rust and of the host is the cause of the reaction, for the growth of hyphae across the surface of the cells produces no apparent effect on the contents of the adjacent cells.

Sometimes haustoria may penetrate into the cell, when the first apparent disturbance in the host is the collection of the protoplasm around the haustorium. This is followed by the disintegration of the nucleus of the host-cell, and then the death of the cell. At the same time the haustorium, mother-cell, and even the hypha back of the latter, are killed. In some instances the rust may continue to send out hyphae, each of which in turn suffers the same fate until the reserve food of the rust is exhausted. In this way there is formed a small amount of dead hyphae surrounded by dead host-cells. Apparently toxic substances spread to surrounding cells, resulting also in their death. The lesions produced in this type of resistance appear as small light-colored flecks on the surface of the host.

Where the resistance is not quite so pronounced the haustorium is able to persist for a time, evidently obtaining some food from the host-cell. Some mycelium may thus be developed before the death of the rust and host-cells occurs, and the areas killed are consequently larger. In different hosts various types of resistance are found (p. 256), evidently depending on the rapidity with which death occurs.

Conditions affecting infection. — The entrance of the haustorium into the cell of its host is brought about either by an enzymatic action dissolving the cell-wall, or by the mechanical puncturing of the wall. In either case, the composition of the cell-wall may play a part in determining whether the haustorium can penetrate or not. It is to be noted, however, that there is no good evidence to show that chemical or physical composition of the cell-wall actually prevents entrance of the haustorium, although several investigators have sug-

gested that such may be the fact, especially where cell-walls have been impregnated with silica.

The osmotic pressure of the cells in both host and rust may also play an important rôle. It is evident that the osmotic pressure of the rust must be higher than that of the host in order that it may be able to withdraw nutrients from the host-cell. Although it is certain that the osmotic action must take place through the plasma membrances of both the host-cell and of the haustorium, yet when killing solutions of strengths just strong enough to plasmolyze the host-cells are used no apparent effect is produced on cells of the rust (Allen, 1923a).

That temperature may be a factor of some importance in infection is indicated by the results obtained by Peltier (1923). By inoculating and keeping different varieties of wheat at various temperatures for 48 hours, and then subjecting them to the same temperature, he found that some varieties of wheat had a more limited range of temperatures at which they would become infected by *Puccinia graminis tritici*, than other varieties. A resistant variety may be as heavily or more heavily infected (p. 231) than a susceptible variety for as great a range of temperatures. Thus Khapli, a highly resistant variety, gave slightly greater infection at 15°, 20°, 25° and 30° C. than did Little Club, a very susceptible variety. His data also indicate that for one strain of the rust, "IX," the temperature range suitable for infection was 5° lower than for another strain, "III," the optimum being 20° C. in the first case, and 25° C. in the second. It is not certain, however, whether this may not be due to the difference in percentage of spore germination of the two strains of the rust at these temperatures. The results obtained by Hursh (1922) with two other strains of this same rust indicate that the latter is likely to be the explanation.

Several investigators have noted that the maturity of hosts has a decided influence on infection. Seedlings of the onion (*Allium cepa*) have been found (Sheldon, 1905) to be completely immune to *Puccinia asparagi*, but when about two months old are favorable for the development of the aecia. The leaves of the apple are susceptible to *Gymnosporangium juniperi-virginianae* from the time of unrolling until 15 to 24 days after unrolling when they become immune (Giddings, 1918). A contrasting period of immunity against *Cronartium ribicola* is shown by young leaves of Ribes (Raines, 1922). As in all the cases cited the criterion of infection apparently was whether or not sori were produced. It is not evident, however, whether maturity actually prevented infection, or whether infection took place and the conditions of maturity

prevented the mycelium from developing to a noticeable extent. In some species of Mahonia and Berberis the cuticle of the young leaves has been found experimentally to thicken sufficiently within a few days to prevent penetration of basidiosporic germ-tubes (Melander & Craigie, 1927).

On the other hand systemic infection probably takes place in the very young tissues of nascent buds, as has been found to be true for *Gymnoconia interstitialis* (Dodge, 1923c), and may be true of other, if not all instances of systemic infection.

DEVELOPMENT OF THE MYCELIUM

Process of development. — The development of the mycelium in several species has been worked out in considerable detail by a number of investigators. Following the entrance of a haustorium into a cell of a favorable host and the resulting establishment of a food connection, the development of hyphae continues and other cells are invaded. The spread of the resulting mycelium varies with different species of rusts. In many instances a more or less localized mycelium is produced, restricted in growth to areas of only a few square centimeters, especially in leaf-inhabiting forms. In others it may develop throughout areas of considerable size, as in the gall-forming aecia of Cronartium. In other instances it may become systemic and cause disturbances in the growing point of the host, which result in witches' brooms.

While the process of mycelial development must necessarily vary somewhat among the widely diverging species of rusts, yet the general development is much the same. Infection of a susceptible host is followed by a period of activity on the part of the rust. New secondary hyphae are constantly budding and growing across the surface of the host-cells until they in turn meet a host-cell and form a haustorium. This process goes on with considerable rapidity, soon resulting in the formation of an intertwined mass of hyphae more or less completely filling the intercellular cavities in the region immediately surrounding the point of entrance.

In the development of the uredinial mycelium of *Puccinia graminis tritici* (Allen, 1923b) the rust enters upon its second phase of development by starting to form the fruiting bodies, primary uredinia, from the mycelial mass, which is rich in protoplasm and food. At the same time stolon-like hyphae are sent out which "unlike the earlier hyphae do not feel their way along the surface of the cells, conforming closely

to their irregularities, nor do they form a haustorium whenever the tip strikes against a host-cell. These well-fed, rapidly growing, sparsely septate stolon-like hyphae strike out away from the center of infection, growing across the intercellular spaces as straight as the irregular passageways of the leaf permit. When they reach fresh tissues, they start new centers of sporulation, which produce a circle of secondary uredinia around the first." The same process may produce one or more circles outside of the first circle (Fig. 132). A similar development has been described for *P. glumarum* and *P. dispersa* (Ward, 1903b; Evans, 1907), and for *Uromyces appendiculatus* (Waters, 1926). In rusts of this localized type there is not much further extension of the uredinial mycelium.

Fig. 132. — Circles of uredinia outside of the primary uredinium of *P. rubigo-vera tritici*. (Original; photograph by Mains.)

In the development in pine needles of the aecial mycelium of *Cronartium ribicola*, Clinton and McCormick (1919) found that the mycelium forms very compact masses in the intercellular spaces, giving somewhat the appearance of sclerotia. They suggest that these masses may act as storehouses of food through the winter months to supply the fungus when it starts growth in the spring. From the mesophyll of the leaf the hyphae penetrate the endodermis of the vascular system, and develop in the phloëm. Strands of mycelium grow longitudinally through the vascular bundle toward the base of the leaf. At the base of the leaf the mycelium spreads out into the cortex

of the branch and develops haustoria in the host-cells. A considerable mass of mycelium results from which the cortical pycnia and aecia eventually arise.

When the mycelium becomes systemic it passes from the place of initial infection into the stem, or even into the underground parts. The mycelium develops along with the new parts of the plant,

FIG. 133. — Three shoots of *Tithymalus cyparissias* from a plant with hibernating mycelium of *Uromyces pisi*, which had been brought into a warm greenhouse shortly after growth began; the host has resumed normal growth free from the fungus. (After Tischler, 1911.)

follows the growing point of shoots and branches and extends into the forming leaves. It is then that the leaves of infested plants are fairly uniformly covered with the sori, as in *Uromyces pisi* (Tischler, 1911) and *Kunkelia nitens* (Dodge, 1923c).

The mycelium in systemic invasion develops in the meristem, following closely the advance of the growing point. When hibernating plants, or those that have recently started to grow, which are infected with *Uromyces pisi*, are brought into the moist and warm atmosphere of the greenhouse, 25 to 27° C., the mycelium in the meristem ceases to advance

(Tischler, 1911), and the shoot develops normally and free of the fungus (Fig. 133).

The period during which the mycelium is developing, *i.e.*, from infection to sporulation, is known as the incubation period. As generally used the term covers the period from the time when the plant is inoculated until the first resulting sori break through the epidermis. This period varies considerably with different rusts. Thus in the cereal rusts, such as *Puccinia graminis, P. rubigo-vera tritici, P. glumarum*, etc., under favorable conditions only from 6 to 10 days are necessary after infection before uredinia are formed. In some other rusts, as for example *Gymnoconia interstitialis*, the infection results from aeciospores in the spring and the telia appear in late summer, an incubation period of about two months. In a number of the systemic rusts infection takes place in the late summer or fall and sori develop the next spring after about six months incubation, as for example, in *Puccinia eatoniae.* Or, when infection takes place in the spring, as in *Kunkelia nitens*, telia appear the next spring, attaining an incubation period of one year. For *Cronartium ribicola*, Clinton and McCormick (1919) give the cycle of development as follows: 1st year, infection in late summer or fall developing compact, mycelial masses; 2nd year, extension from the leaves into the stem and formation of masses of mycelium; 3rd year, pycnia formed during summer; 4th year, aecia formed. In this species the incubation period up to the formation of pycnia is two years, and until the formation of aecia is three years.

Eriksson (1896, 1910, 1922) believes that the rusts not only produce a mycelium, but that sometimes, especially in *Puccinia glumarum* and other cereal rusts, they are to be found in the plant in a state to which he has given the term "mycoplasm." In this condition, their protoplasm is intermingled with the protoplasm of the host, from which, after the winter has passed, it emerges into the intercellular spaces and forms hyphae and haustoria. Sporulation then follows in the usual way. This theory has not met with much acceptance, and is generally considered to be without sufficient foundation (Bolley, 1898; Ward, 1903a, b; Klebahn, 1904a, b). The phenomena cited by Eriksson to uphold his theory are now explained in accordance with facts that do not controvert the generally accepted procedure (Allen, 1928).

Nutrients necessary for development. — The exact nature of the food supply of the rusts is largely unknown. So far, the rusts have not been grown on a non-living medium. They are apparently not able to form a mycelium independent of the living host when supplied

with sucrose, maltose, dextrose, glycerine, asparagine, leucine, peptone, water extracts of the host, or cooked decoctions, both with and without mineral salts.[1]

In view of these facts, it would be natural to assume that the protoplasm of the host is the substance directly attacked and used as food by the parasite, yet it is evident from the manner of development of the rusts that this is not the correct explanation. As infection of susceptible varieties is not followed by any immediate detrimental effect on the protoplasm of the host, it seems more probable that the nutrients upon which the rust depends are the same as those developed and used by the cells of the host. The rust is then to be considered as subsisting, along with the host, upon the foods elaborated by the cells of the host, which may possibly be temporarily stimulated to greater metabolic activity by the presence of the parasite. The drain of food due to the rust may, indeed, be the principal source of injury to the host, although the clogging of the air spaces and dislocation of host-cells may have some injurious effect. With reduction in the metabolism of the host there apparently follows a corresponding reduction in the growth of the rust.

The close connection with the nutrition of the host is further emphasized by the very evident relationship of rust development to the vigor of the host. It is in the vigorously functioning host or host-part that the rusts find the most favorable conditions for their own development. This is the opposite of the situation which occurs in connection with many facultative parasites, which kill and assimilate the protoplasm, a weakened condition of the host rendering this easier. Many investigators have recognized that the development of the rust is proportional to the vigor of the host (de Bary, 1863a; Ward, 1902c; Arthur, 1903b; Sheldon, 1905; Freeman & Johnson, 1911; Stakman, 1914a; Mains, 1917; Butler, 1918b; Stakman & Levine, 1919; Raines, 1922; Peltier, 1923). It is evident that the vigor of the host does not have to be reduced to a moribund condition before the effect is noticeable on the rust. This may be taken as indicating that the protoplasm of the host *per se* is not the food upon which the rust is directly dependent.

The stable organic substances which serve as storage foods in plant-cells, such as sugars, etc., apparently can not be directly utilized by the

[1] Ray (1901, Compt. Rend. Acad. Sci. Paris **133** : 307; 1903, same **136** : 567) claims to have grown a number of rusts upon decoctions of the host and upon sterilized carrot with the production of mycelium and teliospores. The account of his methods is imperfect, and the results recorded have not been duplicated by other investigators.

rusts, although there is a close correlation between rust development and the carbon metabolism of the host. Ward (1905) found that species of Bromus inoculated with *Puccinia rubigo-vera bromi* developed no rust when the plants were kept in the dark or exposed to light deprived of orange-red rays. *Puccinia graminis* has been found to develop best in fairly high light intensities (Stakman & Levine, 1919; Gassner, 1927). The incubation period of *P. coronata* was found by Fromme (1913) and Mains (1917) to be lengthened approximately equal to the time the host was kept in darkness. *Puccinia sorghi*, however, developed vigorously in darkness upon pieces of etiolated leaves when floated on sugar solutions, but did not develop when the leaves were floated on water or mineral nutrients. When the hosts are deprived of carbon dioxide the development of the rusts is retarded and may finally cease, as shown for *P. glumarum* (Ward, 1905), *P. sorghi* (Mains, 1917) and both *P. coronata* and *P. rubigo-vera tritici* (Gassner, 1927). *Puccinia sorghi* when grown on plants of maize, raised from seed deprived of the endosperm, required a longer period for incubation (Mains, 1917), otherwise the endosperm furnished the necessary food for the host, and the rust developed in nearly the same length of time in darkness as in light.

Rusts have been developed upon etiolated plants grown entirely in darkness (Mains, 1917), and also on chlorotic plants (Raines, 1922), which eliminates chlorophyll as a source of food. Since stable carbohydrates and proteins are not the direct source of food it has been suggested (Fromme, 1913; Mains, 1917) that it may be found in some of the transitory products produced in the formation or decomposition of the carbohydrates or proteins. Or, the rusts may be able to utilize substances only when in a nascent state (Mains, 1917) and in an unstable chemical condition, such as probably occurs in the rapid transition among compounds during their formation and transformation in the plant-cell. Or, the rusts may depend upon some particular one or more of the isomeric forms which probably occur in the many organic compounds in the host. Even saprophytic fungi have been shown by Pasteur to utilize one stereoisomer in preference to another, and it seems probable that in some such necessity may lay the explanation of not only the obligate parasitism of the rusts, but perhaps also, in part at least, their specialization.

Effect of acidity on development. — Acidity has been considered by some investigators as likely to be a principal factor limiting or preventing the development of rusts in their hosts, but this can be true only when the vigor of the plant is reduced and a moribund con-

dition is reached with production of high acidity. The evidence derived from tests of hydrogen-ion concentration does not indicate that acidity is to be considered of importance. Hurd (1923) found that wheat in a stunted and drooping condition gave a hydrogen-ion concentration of 5.48–5.50, while vigorous plants showed 5.98–6.02. If the hydrogen-ion tolerance of the mycelium is the same as that for germination, this difference would have no effect, for Hursh (1922) found that two strains of *P. graminis tritici* have a much greater tolerance than this, germinating through a range of 4.2–7. Hurd also was not able to find a correlation between hydrogen-ion concentration and varietal resistance of wheat to *P. graminis tritici*, to *P. rubigo-vera tritici*, or to *P. glumarum*. In these tests environmental factors produced greater differences in hydrogen-ion concentration of the expressed juice, than were found between different varieties, or between plants of different ages.

Effect of maturity of tissue on development. — That the maturity of the tissues has a marked effect upon the development of the rust is a well recognized fact. However, little is known about the underlying causes. Often with the maturing of the tissue the development of the rust takes place much more slowly, and while producing a mycelium may not reach a condition of sporulation. Sometimes, even infection is prevented. At other times, although infection takes place yet the development of the mycelium is slow and only a weak sporulation occurs. This is especially true with the gametophytic mycelium. Although infection of young leaves and stems may give a vigorous development of mycelium and the resulting production of a large number of aecia, yet infection of older and fully matured leaves of the same plants often results only in a small amount of mycelium and little or no sporulation, pycnia alone being produced or pycnia and a few aecia. A shortened incubation period for *Puccinia asparagi* on young shoots of Asparagus, as compared with the development on older shoots has been noted (Raines, 1922). Older plants of Agropyron and Elymus have proved much less favorable to the development of *P. graminis* than seedlings (Stakman & Piemeisel, 1917).

That the chemistry of a plant changes markedly as it ages is well known, and is substantiated by the investigations of Eckerson[1] on the development of the wheat plant. In these changes doubtless will be found the explanation of some of the differences noted in the development of the rusts in tissues of different maturity.

[1] Eckerson, Sophia H. Microchemical studies in the progressive development of the wheat plant. Bull. Wash. Agr. Exp. Sta. 139, 20 pp., 2 pl. 1917.

SPORULATION

An important principle in the study of rusts was promulgated by de Bary (1865) when he fixed upon the potential number and succession of spore-forms in the life-cycle. It was recognized at the same time that while the spore-forms had an invariable succession, yet any one or more of them, except the last, might be omitted from the cycle, as in fact occurs regularly with many species.

Fig. 134. — Leaf of *Helianthus annuus* showing result of monosporic infection with basidiospores of *Puccinia helianthi:* ten infected spots on the right half of the leaf had the nectar intermixed and show abundant aecia, the six spots on the left half did not have the nectar intermixed and show no aecia. (After Craigie, 1927a.)

Stimulation in the production of aecia has been observed when nectar from one group of pycnia, derived from the growth of a single basidiospore, is mixed with that of another such group. As reported by Craigie (1927b) a leaf of the common sunflower was inoculated on July 9 with basidiospores of *Puccinia helianthi* in such a manner that the spores fell some distance apart. Twenty days afterward the nectar, acting as a vehicle for the pycniospores, was well mixed in ten groups of pycnia on one-half of the leaf, while that in the six groups on the other half of the leaf was stirred in each group separately but not mixed. Five days later the ten groups with intermixed nectar had formed aecia, while the six groups with no interchange of nectar had shown no aecia (Fig. 134). Similar results were obtained with *Puccinia graminis* on barberry. This behavior has been interpreted as the interaction of pycniospores between heterothallic strains of rust, the pycniospores being "unisexual and produce unisexual mycelia" (Craigie, 1927a). When such experiments were kept under further observation, however, it was found that a few of the groups with unmixed nectar eventually produced aecia, but the great majority showed no further development.

Similar tests were made after killing the pycniospores by heating the nectar to 70° C., in which instances no stimulatory action was obtained. It should be noted, however, that these tests did not remove the possibility that the nectar instead of the pycniospores may be held accountable. Enzymes or similar activating substances are known to be present in the nectar, and it is likely they would be destroyed at the temperature employed, as few such substances can withstand more than 35° to 50° C.

That mixing the nectar causes a stimulation in the formation of aecia and aeciospores is beyond question, but the cause remains unexplained. On the one hand no morphologic action of the pycniospores has been demonstrated, and previous knowledge would not lead one to expect such action, and on the other hand the possible stimulation by the presence of enzymes or other activating substances in the nectar has not been proved or disproved.

In submitting the question of sporulation to experimental study, it must be recognized that each species of rust is likely to possess more or less specificity regarding the time of appearance and the abundance of each kind of spore. Not only is this true of species, as evidenced by common observation, but it has been found to be true of varieties and strains of the same species. Working with urediniospores of *Puccinia coronata* strains have been found which produced telia quite generally on most of the varieties of oats tested, other strains were found which produced teliospores on only a few varieties, and still others which did not produce teliospores on any of the varieties (Hoerner, 1919, 1922). In like manner Raines (1922) was able by selection to separate strains of *P. coronata* producing no telia, others producing a moderate number of telia, and a few forming telia only.

Although the balance between urediniospore and teliospore production varies with different species, and even strains, yet there may be said to be normal periods which may be influenced by a variety of factors. Ivanov (1907) found that cool temperatures checked urediniospore production, and increased the development of teliospores. The critical factor in bringing about teliospore formation in *P. asparagi* is considered by Smith (1904) to be humidity, a dry atmosphere preventing urediniospore formation and causing teliospores to develop. Humidity of both air and soil was found by Waters (1928) to increase teliosporic formation in *P. asparagi*. Under cool greenhouse temperatures and poor illumination during winter months teliospores of *P. graminis* were produced in abundance on young plants of rye, and also under these

conditions *P. montanensis* gave abundance of teliospores on seedlings of a number of species of grasses (Mains, 1924a). Resistant varieties of beans have been found to inhibit in part or wholly the production of urediniospores (Fromme & Wingard, 1921; Waters, 1928).

Comparative observations on a number of rusts showed (Gassner, 1915) that teliospores began to be formed in *P. rubigo-vera tritici* shortly before heads of the cereal appear, in *P. coronata* at the time of heading, in *P. graminis* when the plants are about to mature, and in *P. sorghi* when the plants are flowering. In these species the production of teliospores was not hastened by withholding mineral nutrients from the hosts, or mutilating the leaves, as found by Morgenthaler (1910) for *Uromyces veratri.*

Weakening or exhaustion of the host may hasten the production of teliospores (Magnus, 1890; Morgenthaler, 1910; and others). Waters (1928) found in the study of ten species of rusts, when subjected to various kinds of treatment by which the supply of nutriment to the host was restricted, that the production of urediniospores was partly or wholly checked and teliosporic activity increased.

Under these diverse conditions it is probable that instead of a direct influence of the environment upon the rust, an indirect influence is exerted through a change in the metabolism of the host. When the host, or the part of the host supporting the mycelium, furnishes a liberal supply of nutriment for the rust, uredinial production predominates, when the supply of nutriment is restricted telial production is favored (Waters, 1928). This explanation may in part at least account for certain climatic effects, such as the varied behavior of *Uromyces acetosae* in Sweden, in the southern part displaying the full complement of spores, in the central part about Stockholm showing few or no urediniospores, and in the northern part becoming a microcyclic species, *fide* Lagerheim.

In tropical and subtropical regions the predominence of uredinia in many species has often been remarked. It is usually ascribed to the absence of regularly recurring conditions that check growth, as found in temperate and still more northern regions. In support of this explanation an observation by Lagerheim (1894) is often cited. The broad bean, *Vicia faba,* as grown in the gardens at Quito, Ecuador, is affected with *Uromyces fabae,* but only uredinia are produced. Gassner (1915) found by experiment, that if a series of plantings were made in the early part of the season, or if the plants were shaded from the intense sunlight in the latter part of the season, teliospores were obtained, the

explanation being that under tropical conditions the leaves of the host matured and fell so quickly after reaching full size, that the rust did not have a sufficient length of time in which to pass into the teliosporic stage.

When the supply of nutriment or the condition of the host is unfavorable for production of uredinia, the entire uredinial stage may be omitted, the rust going directly from aecia to telia. This has been observed with *Cronartium cerebrum* when aeciospores were sown on mature and firm leaves of *Quercus rubra* (Arthur, 1915). A striking illustration of the effect of mature tissues in suppressing a spore-form has been demonstrated in the case of *Puccinia podophylli* (Whetzel, Jackson & Mains, 1925), a species in which no uredinia occur. When basidiospores were sown on the young rapidly growing leaf blades pycnia and aecia were formed, but when sown on early maturing leaf sheaths, stems, or highly matured leaf blades, telia were formed, and usually without pycnia, thus totally suppressing the aecia. It is considered that here, as in the other instances cited, the food relation is the important factor in changing the course of development. Only the well nourished tissues gave the full complement of spore-forms. With *P. coronata* on oats it has been found that both an unfavorable condition of the host and an increase in the degree of resistance hasten the formation of teliospores (Ruttle & Fraser, 1927).

In all the cases so far mentioned, showing the suppression of a spore-stage other than the pycnial, one of two things must have occurred, either the urediniospores failed to develop on the sporophytic mycelium, or else the entire sporophytic mycelium was suppressed. Pycnia arise from the ever present gametophytic mycelium, and their presence or absence indicates degrees of vigor or a fixed state of development. No authenticated instance is known where the gametophytic mycelium, although it may have become more or less binucleate, has passed directly into the sporophytic mycelium, such transition requiring the intervention of an aeciospore. It therefore follows that the reported suppression of aecia in a macrocyclic species normally possessing a full complement of spore-forms, without disturbance of the other spore-stages, must be taken *cum grano salis*, as requiring special explanation. Thus, the instances where *Puccinia helianthi* failed to produce aecia, the pycnia being associated with the uredinia (Carleton, 1904; Bailey, 1923), require further illumination before they acquire significance.

Much information has been accumulated regarding the factors that tend to stimulate or reduce the production of any one stage of the rusts

in its proper succession, but no explanation is available to account for the production of one form of spore rather than another at any particular stage.

FACTORS AFFECTING THE RUST INDIRECTLY THROUGH THE HOST

The effect of the host's environmental conditions upon the development of the mycelium of the rust is probably for the most part indirect. Whatever makes for the betterment or detriment of the host is likely to be reflected to some extent in the activity of the rust. Some study of the outside factors in their relation to growth of the rust has been made, especially of the mineral nutrients, water and temperature.

Mineral nutrients. — In a series of water cultures, using corn (maize) and Knop's nutrient solution, with the endosperm removed from part of the seeds after appearance of the first leaf, *Puccinia sorghi* showed a longer incubation period and appreciably smaller uredinia containing fewer spores coincident with depression in the vigor of the host (Raines, 1922). The same general results followed in tests with *Puccinia coronata* on oats grown in 2-inch pots with mineral fertilizers. Decreasing the supply of the nutrient by increasing the number of plants in a pot, or otherwise, decreased the number of uredinial sori (Raines, *l.c.*). Deficiencies in the essential plant elements, calcium, magnesium, potassium, phosphorus, nitrogen, iron, chlorine and sulphur, do not prevent the mycelium from developing and sporulating, yet the development of the rust in all instances is decreased, agreeing in general with the vigor of the host (Ward, 1902b; Stakman, 1914a; Mains, 1917; and many others). In a series of sand cultures, using Marquis wheat, the addition of the chlorides of potassium, calcium, or magnesium, caused a marked decrease in the amount of rust, while 2.05 grams of sodium superphosphate to the liter caused a slight increase, but half the amount caused some decrease (Weiss, 1924).

In studying the effect of salts of lithium, zinc and copper, it has been found that most lithium salts are detrimental, yet lithium nitrate stimulates development. Zinc salts usually give increased development, especially zinc nitrate (Voelcker, 1912; Spinks, 1913). Copper sulphate and copper carbonate, when used in concentrations which do not prevent the normal development of the host, do not appreciably decrease the amount of rust (Stakman, 1914a). Copper sulphate applied to the soil apparently reduced the development of *Puccinia malvacearum* during the earlier part of the season, but not later (Eriksson & Hammarlund, 1914; Eriksson, 1922).

It has been repeatedly observed that rich nitrogenous fertilizers are conducive to increased vegetative development on the part of host and rust alike. The addition of sodium nitrate to a full mineral nutrient in sand culture almost doubled the amount of rust on Marquis wheat (Weiss, 1924), while even the nitrates of lithium and zinc increase the amount of rust, as previously noted.

Water. — Many field observations have indicated that high atmospheric humidity and wet soils favor rust development. Part of the observed effect is likely due to the influence on spore germination. Some evidence indicates that these conditions influence mycelial development. De Bary (1863a) found that the vegetative development of *Uromyces appendiculatus* was greatly increased by a humid atmosphere. Smith (1904) considered that a dry atmosphere retarded the development of the rust within the host. Mains (1917) found that a humid atmosphere favored the development of *Puccinia sorghi.*

Soil moisture evidently has an effect on rust development, although there is a difference of opinion as to the manner of its action, which possibly may be explained in part by a specificity on the part of the host. In some experiments dryness of soil has been found favorable to the rust (Stone & Smith, 1899; Smith, 1904; Blaringhem, 1912), while in other instances a wet soil has been found more conducive (Sirrine, 1900; Buchet, 1913; Mains, 1917; Stakman & Levine, 1919).

Illuminating results have been obtained in experiments on the relation of water content of soils to infection in *Puccinia graminis* (Stakman, 1914a). Iumillio and Kubanka, two drought resistant varieties of wheat, rusted more when the soil was relatively dry, while Minnesota No. 163, a mesophyte, showed somewhat more rust when the soil was wet. The conclusion to be drawn is that the water relation which is most favorable for the development of the host is also the most favorable for the rust.

Temperature. — It is difficult to differentiate any direct effect of temperature on the development of the rust as distinct from the effect produced on it through the action on the host. Apparently the rapidity of development of the rust, as measured by the length of its incubation period, increases with rise in temperature, *i.e.*, the period becomes shorter, until the point is reached at which the metabolism of its host is impaired. The incubation period of *Puccinia coronata* has been found to be twelve days with the temperature at 14.5 to 21° C., and seven days at 20 to 30° C. (Fromme, 1913), while that of *P. sorghi* was thirteen days at 13° C., and seven days at 18 to 20° C., and at 30° no uredinia

were developed at the end of fourteen days and only a sparse amount of mycelium (Mains, 1917).

The optimum temperature for the incubation period of *Puccinia graminis tritici* was found to be 19 to 21° C. (66.5 to 70° F.) with an incubation period of six to eight days. The incubation period was longer by one day for each 5.5° C. (10° F.) in rise of temperature, or the same for half as much in fall of temperature. Infection resulted at as high and also at as low temperatures as the host endured (Stakman & Levine, 1919). In another series of tests with the same variety of rust, although not the same strains, the incubation period ranged in 5° intervals from eighteen days at 10° C., sixteen days at 15° C., eleven days at 20° C., to eight days at 25 to 30° C. Inoculated plants held at 5° C. for nine weeks showed no apparent infection, but developed rust when transferred into higher temperature (Peltier, 1923). Observations in the field have indicated a similar influence (Christman, 1905b). Although the mycelium can doubtless endure as low temperatures as the host within which it thrives, yet high temperatures may be reached that are detrimental to the rust without much injury to the host (Ward, 1902a).

SECRETIONS AND RESERVE FOODS

But little study has been given to the substances secreted by the rusts. One of the most conspicuous and best known secretions is the sugary solution, or nectar, most usually observed accompanying pycnia (p. 11). It is sweetish to the taste, reduces Fehling's solution, and probably contains a mixture of sugars (Ráthay, 1883). This solution is often produced in such quantity that it falls in drops from the host, especially in a humid atmosphere. It is attractive to insects (Ráthay, 1883; Shear, 1906; Grove, 1913b; Meinecke, 1920; Spaulding, 1922; Craigie, 1927b), and to various animals that are fond of sweets.

Pycnia also give off an odor that is often readily noticed, sometimes it may be even before the presence of the rust is detected (Klebahn, 1904a). It is, by most persons, considered a pleasant fragrance, and has been likened to that of orange blossoms (Léveillé, 1846), evening primrose (de Bary, 1853), willow pollen (Tulasne, 1854b), tea-rose (Schaffnit, 1909), and hyacinth (Jackson & Mains, 1921). *Puccinia suaveolens*, occurring on *Cirsium arvense*, was so named by Persoon (1801) on account of its odor, which he considered distinctive. Link (1825) thought this odor disagreeable. That the odor associated with the rusts is a product of the mycelium rather than of the sori was

first pointed out by Klebahn (1900), who observed that in *Pucciniastrum padi* on spruce the fragrance was observable some considerable time before the pycnia made their appearance. The same odor has also been noticed with aecia and uredinia when confined for a time in a closed dish (Schaffnit, 1909).

The characteristic coloring matter of rusts, which is a bright-yellow varying to golden-yellow in many basidiospores, aeciospores and urediniospores, and becomes a yellowish-red or reddish-brown in some spores, particularly in teliospores, has never been fully studied. It has been thought from some preliminary studies that there are two chemically distinct substances (Dietel, 1891), and that the yellow color of the spore is due to xanthin, as it may be extracted with ethyl alcohol as an oily resinous substance, quickly decolorized by light (Schaffnit, 1909). Extracts made with carbon bisulphide and examined with a Hilger spectrometer indicate carotin. A variety of tests have failed to extract the red coloring matter from the spore-walls, but indicate that it is neither carotin, xanthophyll, lycopin, nor rhodoxanthin, in fact not a carotinoid (Newton & Johnson, 1927b). From the meager direct information yet available, both microscopic and chemical, one may infer that all rusts possess a yellow substance in the cytoplasm, when it shows any color at all, held in solution by the oil drops, and which like the oil serves as a reserve nutrient. The cell-wall of many spores contains a red coloring matter, which is more concentrated the deeper the color of the spores. The blending of the yellow of the cytoplasm and the red of the walls gives all the varying hues known for the rusts.

Practically nothing is directly known concerning the existence of enzymes in the rusts. Although various toxins are supposed to be excreted yet no one has even suggested the nature of such products.

CHAPTER VII

SPECIALIZATION

Specialization of species: range of hosts; physiologic races, physiologic forms.

Reaction as a means of classification: correlation between susceptibility and immunity, factors governing compatibility.

Nature of resistance and susceptibility: cytologic evidence; genetic evidence in connection with forms, grafts and chimeras; morphologic evidence; physiologic evidence; variety and combination of factors.

Stability of reaction: in the rust, "bridging hosts," possibility of hybrids and mutations; changing conditions in the host.

One of the phases in the investigation of rusts which is being given an increasing amount of attention is the specialization of these fungi to a more or less limited number of hosts. As a group the rusts are restricted in that they require living plants for development and also in that they are found only upon members of the pteridophytes and spermatophytes.

SPECIALIZATION OF SPECIES

It was early noted that rusts differ from each other in the species of hosts which they parasitize, and furthermore that the rusts of like morphology are usually found upon more or less closely related hosts. The recognition of the obligate parasitism of the rusts early influenced the conception of species and of their limitations. This resulted in the tendency to confine the comparison of rusts in taxonomic studies to those upon closely related genera. Following the discovery that even within morphologically similar groups, there exist smaller specialized groups which differ in their hosts, the particular idea of specialization further modified the species concept. Some investigators have based species mostly on likeness in morphology, and others on similarity in the selection of hosts. The subdivisions, varieties, races, forms, etc., of some taxonomists often become species in the treatment by others. In making comparisons of species these differences in concept must be kept in mind.

With similarity in morphology as a basis for grouping, species differ widely in the range of hosts on which they are recorded. Some species are recorded for a fairly wide range. Thus among the autoecious rusts,

Puccinia malvacearum is listed on 40 species belonging to 8 genera of the Malvaceae (Sydow, 1902–04), and *P. grindeliae* is given on 87 species of 24 genera of the Carduaceae (Arthur & Jackson, 1922). Among the heteroecious rusts, usually the hosts for the two phases of the life-cycle are members of widely separated families. Thus in the genus Coleosporium the gametophytic phase is produced upon species of Pinus, while the sporophytic phase may develop upon species of the Carduaceae, Campanulaceae, Convolvulaceae, Grossulariaceae, etc. Species of Gymnosporangium develop their gametophyte largely on Rosaceae while their sporophyte is mostly restricted to species of the Cupressineae.

While the two phases of heteroecious species are usually found on hosts of widely separated relationship, such rusts also differ considerably in the range of each of the phases. Some species have a wide range for the gametophytic phase and a restricted range for the sporophytic, while others show the reverse habit. *Puccinia graminis* develops its gametophyte on a few species of Berberis and Mahonia, while its sporophyte occurs upon 98 species of 35 genera of the Poaceae in North America alone (Arthur & Fromme, 1920). *P. subnitens* on the other hand largely occurs as a sporophyte on one species of grass, *Distichlis spicata,* while its gametophyte is developed on hosts belonging to 90 species of 64 genera and 24 families (Arthur & Fromme, 1920).

Some heteroecious species are listed as occurring on a fairly wide range of species for both phases of their life-cycle. Thus the gametophytic phase of *P. coronata* is given (Arthur & Fromme, 1920) as occurring on 10 species in 4 genera and 2 families, Rhamnaceae and Elaeagnaceae, and the sporophyte as on 40 species in 21 genera of the family Poaceae. The same authors list the gametophytic stage of *P. clematidis* on 59 species of 14 genera of the Ranunculaceae and the sporophytic on 92 species of 17 genera of the Poaceae. If, as more recently suggested (Mains & Jackson, 1926), the latter species be considered as only a part of *P. rubigo-vera,* the host range for the gametophyte would be still more extended, including genera of the Ranunculaceae, Boraginaceae, Balsaminaceae and Hydrophyllaceae, and the range for the sporophyte on Poaceae also would be more extended.

While heteroecious rusts may be found on a fairly wide range of hosts in one or both of their phases, some species are restricted to only a few hosts in both phases. Thus the leaf rust of barley, *P. anomala,* develops its gametophyte on Ornithogalum and its sporophyte only on cultivated barley.

Among autoecious species, there may be restriction to species of a

single genus, as in *P. cirsii* on 41 species of the genus Cirsium and *P. violae* on 45 species of the genus Viola. Or the restriction may be to one species, as in the case of *P. suaveolens* on *Cirsium arvense* and *P. buxi* on *Buxus sempervirens.*

Physiologic races. — Not only do the rusts, classified largely upon a morphologic basis, differ widely in the species of hosts upon which they are found, but it is possible to subdivide many such species into groups distinguished largely or solely by the hosts which they can infect. The extensive studies of Eriksson (1894, 1896, 1897c, 1898a, b, 1899, 1902, 1909) and Eriksson and Henning (1894, 1896) not only threw considerable light on this question but stimulated similar study of additional species of rusts by other investigators.

Various terms have been applied to the groups which are distinguished largely by their choice of hosts (p. 104), such as "sister species," "biologic species," "physiological species," "adapted races," and "biologic races." Eriksson's preference (1894) was the term "specialized forms" (*specialisierte Formen* or *formae speciales*), which has been modified by Ward (1905), Stakman (1914a), and others to "biologic forms." A resolution adopted by the American Phytopathological Society (Shear, 1925) recommends the term "physiologic form." In the present work the term physiologic race will be used, and for its subdivision the term physiologic form. It is to be noted that such various designations as forms, races and species have been employed with a difference of opinion concerning the rank of such groups in classification.

The host specialization of *Puccinia graminis* has received by far the most study. As the result of the investigations of Eriksson (1894, 1897c, 1898a, 1902), Jaczewski (1910), Carleton (1899, 1904), Freeman and Johnson (1911), Arthur (1902a, 1904c, 1906b, 1907, 1908a, 1910b, 1912), Stakman (1914a, b, 1915), Stakman, Parker and Piemeisel (1918), Stakman, Levine and Bailey (1923), Stakman and Piemeisel (1916a, b, 1917), Stakman and Levine (1919, 1922), Stakman and Aamodt (1924), Stakman, Levine and Griffee (1925), and others, this species has been studied in many different climatic regions and under varying conditions. Eriksson divided the species into seven races in accordance with the species of grass hosts which he found to favor the development of its sporophytic mycelium. Extensive studies by a number of other investigators have added further information concerning the range of hosts for the several races, and also resulted in the discovery of additional races. The combined results of these studies indicate that the various races differ considerably in their sporophytic stage, not only in the genera of grasses

which they are able to infect, but also in the range of species among the several genera.

While *P. graminis* can be separated into a number of different races on the sporophytic side, not so much is known concerning the development of its gametophyte. Apparently *Berberis vulgaris* is a favorable host for all except one of the races recognized in the sporophytic stage. For the one exception, *P. graminis phlei-pratensis*, a congenial aecial host is unknown, for this race differs from the others in not infecting *Berberis vulgaris* to any extent. Whether races can be distinguished by any of the other species of Berberis, known to be hosts for this rust, can not be stated from the information at hand. The separation of the race on *Phleum pratense* and its elevation to the rank of a distinct species, *P. phlei-pratensis*, was done largely for the reason that *Berberis vulgaris* was not a favorable aecial host, as in the case of the other races.

Apparently much greater importance is sometimes attached to differences shown in the selection of the aecial hosts than of the telial. Thus Klebahn (1895, 1896) separated the crown rust of grasses, *P. coronata* of Corda into two species *P. coronifera* and *P. coronata* (emend.), largely on the basis that the former produces its aecia on one group of species of Rhamnus while the latter develops aecia upon another group. Additional allied species have been recognized on the same basis (Mühlethaler, 1910, 1911). Within these species, however, there are several recognized races which are markedly specialized to grass hosts of separate genera. Thus, there is a race apparently limited to *Holcus lanatus* and another to a few species of Calamagrostis. Since both of these races produce aecia on *Rhamnus frangula*, they are considered (Klebahn, 1896, 1904a) to be the races *holci* and *calamagrostidis* of the species *P. coronata*, while a rust limited to *Holcus lanatus* and *H. mollis*, but producing its aecia on *Rhamnus cathartica*, is considered as the *holci* race of another species *P. coronifera*. Other investigators (Arthur & Fromme, 1920; Melhus, Dietz & Willey, 1922) prefer to retain all of these as races under one species, *P. coronata* of Corda.

Another rust which shows interesting differences in host specialization is *P. dispersa* of Eriksson and Henning. It was found (Eriksson & Henning, 1894) that this rust could be separated into four races (1) *secalis* on *Secale cereale*, (2) *tritici* on *Triticum vulgare*, (3) *bromi* on *Bromus arvensis* and *B. brizaeformis* and (4) *agropyri* on *Agropyron repens*. Further investigations showed that these races are all much limited in their range, each being confined to species within the one genus, and *agropyri* apparently even being restricted to one species of host, *Agropy-*

ron repens. Eriksson (1899) raised the several races to specific rank, partly on the assumption that they differed in aecial hosts, although at the time only the aecia of *P. dispersa secalis* were known, which occur on species of Anchusa. Later investigators have shown that *P. dispersa tritici* produces aecia on species of Thalictrum (Jackson & Mains, 1921), and *P. dispersa bromi* on species of Symphytum and Pulmonaria (Müller, 1901). In converting the races into species Eriksson retained the name *P. dispersa* for the *secalis* race, and named the *tritici* race, *Puccinia triticina,* the *bromi* race, *P. bromina,* and the *agropyri* race *P. agropyrina.* Arthur and Fromme (1920) considered that most of the races having aecia on Ranunculaceae belong to the species *P. clematidis,* to which Cunningham (1923) has agreed but considers the name should be *P. elymi.* Mains and Jackson (1926) have suggested that all the races, and even the similar ones having Boraginaceous and Hydrophyllaceous hosts, should be recombined under the older name of *P. rubigo-vera.*

By accepting the last concept the species, *P. rubigo-vera,* would consist of a fairly large number of races, each of which would be more or less narrowly restricted to a few closely related species of hosts for the development of both the sporophytic and gametophytic mycelia. The restriction differs for the different races. In some races as in *agropyri* (*P. agropyrina*) apparently only one species, *Agropyron repens,* is its sporophytic host and one species, *Thalictrum flavum,* its gametophytic host. In other races both the sporophytic and gametophytic stages may be able to develop upon several species of hosts, as in the race *tritici* (*P. triticina*). The most extensive host range in this collective species so far noted is in the race *P. rubigo-vera actaeae-elymi,* which, although restricted to *Elymus europaeus* for its sporophytic stage, is able to produce its aecia upon 20 species of the genera Actaea, Aconitum, Delphinium, Eranthis, Helleborus, Isopyrum and Nigella (Mayor, 1920).

Among autoecious rusts there are species in which the races are restricted to different species of the same genus of hosts. Such rusts are *Melampsora euphorbiae* (Müller, 1906, 1907), *M. euphorbiae-dulcis* (Müller, 1906, 1907; Klebahn, 1912–14), *Phragmidium disciflorum* (Bandi, 1903), *Puccinia leontodontis* (Probst, 1908), *P. hieracii* (Jacky, 1899; Probst, 1909), *P. ribis* (Eriksson, 1898b), *P. helianthi* (Arthur, 1903c, 1904c, 1905a, 1906b; Kellerman, 1903, 1905; Jacky, 1902; Bailey, 1923), *P. centaureae* (Jacky, 1899; Hasler, 1908), *P. carduorum* (Probst, 1908), *Uromyces proëminens* (Arthur, 1900b, 1902a, 1903c), and *U. trifolii* (Kobel, 1920; Davis, 1924). In a few autoecious species the races are found upon different genera. Such rusts are *Puccinia*

epilobii-tetragoni (Arthur, 1907–27), *Uromyces fabae* (Jordi, 1903, 1904), and *U. appendiculatus* (Fromme & Wingard, 1921).

Physiologic forms. — Rusts not only may be distinguished by the species of hosts in which they are able to develop, but may be separated by their behavior toward the several varieties of such species. Through the studies of Stakman and Levine (1922) it has been shown that some of the races of *Puccinia graminis* can be still further segregated by differences in behavior on certain cultivated varieties of the cereals. Thus *P. graminis tritici* consists of at least 37 physiologic forms differing in ability to parasitize 12 agronomic varieties of Triticum. The differences used to distinguish such forms may be illustrated by the behavior of four of these physiologic forms upon three varieties of wheat, Little Club, "C. I. 4066,"[1] Marquis, "C. I. 3641," and Kanred, "C. I. 5146." They find that Little Club and Marquis are more or less susceptible to physiologic "form 1" while Kanred is highly resistant. To physiologic "form 33" Little Club and Kanred are susceptible while Marquis is moderately resistant. To physiologic "form 4" Little Club is susceptible while both Marquis and Kanred are resistant. To physiologic "form 11," all three varieties are susceptible. In a similar way using three varieties of oats four physiologic forms in *P. graminis avenae* have been distinguished (Stakman, Levine & Bailey, 1923), and also evidences indicating the existence of three or four physiologic forms in *P. graminis secalis* (Levine & Stakman, 1923). In the Dominion Rust Research Laboratory at Winnipeg, Canada, six physiologic forms of *P. graminis avenae* were found during the study of a large number of varieties and strains of oats received from various parts of Europe and North America (Gordon, 1928; Gordon & Bailey, 1928).

Such physiologic forms are not confined to *Puccinia graminis*. Twelve physiologic forms in the leaf rust of wheat (*P. rubigo-vera tritici*), as differentiated by the reaction of eleven lines of wheat (Table 16), have been distinguished in the United States (Mains & Jackson, 1926), and four physiologic forms in Germany (Scheibe, 1928), only one of the latter being identical with one in America. Four physiologic forms in *P. sorghi*, as distinguished by the reaction of three inbred lines of maize, are reported by Mains (1926b), while Stakman, Christensen and Brewbaker (1928) report seven physiologic forms in the same rust. Two such physiologic forms have been distinguished in the leaf rust of rye, *P. rubigo-vera secalis*, and two in the leaf rust of barley, *P. anomala* (Mains, 1926b).

[1] Refers to the record numbers in the Office of Cereal Crops and Diseases, U. S. Department of Agriculture.

Four physiologic forms of the crown rust of oats, *P. coronata avenae*, as distinguished by the reaction of five or more varieties of oats, have also been reported (Hoerner, 1919; Parson, 1927).

TABLE 16 — TYPES* OF INFECTION PRODUCED BY TWELVE PHYSIOLOGIC FORMS OF THE LEAF RUST OF WHEAT, *Puccinia rubigo-vera tritici* (*P. triticina*), ON ELEVEN DIFFERENTIAL STRAINS OF WHEAT.

Varieties of Wheat	Types of Infection Produced by Physiologic Forms											
	1	2	3	4	5	6	7	8	9	10	11	12
Malakoff, C. I. 4898.....	0	0–1	0–1	0–1	4	4	4	4	4	4	0	0
Turkey, 47.....	0	0–1	0–1	0–1	4	4	4	4	4	4	0	0
Norka, C. I. 4377.....	0	0–1	0–1	0–1	4	4	4	4	4	4	0	0
Unnamed, C. I. 3756....	0	0–1	0–2	4	0	2	1–2	1	1–2	4	2+	4
" C. I. 3778....	0	0–1	2–2+	4	0–1	4	1	4	1–2	4	3–4	4
Webster, C. I. 3780.....	0	0	0–2	1	0–1	1–2	4	4	4	4	1–2+	1
Unnamed, C. I. 3747....	0	0	0–2	1–2	0–1	1	4	4	4	3–4	1–2+	0–1
" C. I. 3779....	0	0–1	3–4	3–4	0–1	3	1	4	4	4	3–4	4
Mediterranean, C. I. 3332	1	4	3–4	3–4	4	3–4	4	3–4	0–1	1–2	1–2	4
Hussar, C. I. 4843.....	1	3–4	0–1	2–2+	0–2+	3	1	1	1–2+	1–2	0–2	4
Democrat, C. I. 3384....	0	4	4	1–2	4	3–4	4	1	0–1	1–2	0–2	4

* The types of reaction shown by the differential varieties to these twelve physiologic forms are described by Mains and Jackson (1926) as follows:

0. *Highly resistant;* no uredinia formed, small flecks, chlorotic or necrotic areas more or less prevalent.
1. *Very resistant;* uredinia few, small, always in small necrotic spots. Also more or less necrotic areas produced without development of uredinia.
2. *Moderately resistant;* uredinia fairly abundant, of moderate size, always in necrotic or very chlorotic spots. Necrotic spots seldom without uredinia.
3. *Moderately susceptible;* uredinia fairly abundant, of moderate size. No necrosis produced, but sometimes slight chlorosis immediately surrounding the uredinia.
4. *Very susceptible;* uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occurring as green islands surrounded in each case by a chlorotic ring.

Whether physiologic forms exist in all species of rusts cannot at present be stated, for too few species have been critically studied with this type of specialization in mind. Using 16 clonal lines of timothy resistant to *P. graminis phlei-pratensis*, Barker and Hayes (1924) were unable to obtain evidence of the existence of physiologic forms in this rust. Negative evidence is not, however, conclusive, since more varieties may be necessary to distinguish between forms, or the physiologic forms may be few and localized in widely separated localities. While the negative evidence is inconclusive it does indicate that

physiologic forms probably are not so common in some species as in others.

The parasitic capacities of the various physiologic forms may vary considerably. Thus, according to Stakman and Levine (1922), to one physiologic form of *P. graminis tritici* eleven of the differential varieties are susceptible and one resistant; to two forms, ten varieties are susceptible and two resistant; to four forms nine varieties are susceptible and three resistant; to seven forms eight varieties are susceptible and four resistant; to six forms seven varieties are susceptible and five resistant; to seven forms six varieties are susceptible and six resistant; to two forms five varieties are susceptible and seven resistant; to seven forms, four varieties are susceptible and eight resistant; and to one form three varieties are susceptible and nine resistant. Somewhat similar differences exist between the various physiologic forms of *P. rubigo-vera tritici* (Mains & Jackson, 1926), as shown in Table 16.

While the 37 physiologic forms of *P. graminis tritici*, designated by Stakman and Levine (1922) as occurring on certain agronomic varieties of wheat (p. 255), show a remarkable specialization of this race within the genus Triticum, yet some at least of these physiologic forms find congenial hosts on a fairly wide range of wild grasses of different genera, as indicated by previous studies (Stakman & Piemeisel, 1917). The leaf rust of wheat, *P. rubigo-vera tritici*, on the other hand, is mostly restricted to the genus Triticum.

It has been discovered in selecting hosts for critical study of the rusts (Mains & Jackson, 1926) that physiologic forms may be selective within agronomic varieties of wheat. Thus in the variety Turkey some lines are highly resistant while others are highly susceptible. Thus, *P. rubigo-vera tritici* "physiologic form 3" can be easily distinguished from "p. f. 5" by a line (C. I. 4898) of an agronomic strain (Malakoff) of a variety (Turkey) of *Triticum vulgare*, this line being highly resistant to "p. f. 3," and highly susceptible to "p. f. 5."

The ability to distinguish physiologic forms depends upon the discovery of the proper differentiating hosts. Many wheat lines are susceptible to all physiologic forms of leaf rust and with such, therefore, the various physiologic forms are not distinguishable. The characterization of physiologic forms depends therefore on the characteristics of the hosts used. Using wheat, rye, and a number of wild grasses Eriksson and Henning (1894) were able to distinguish a race (*P. triticina*) of *P. rubigo-vera* limited to wheat. While studying this race Mains and

Jackson (1926) found (Table 16) that a line of wheat (Malakoff "C. I. 4898") was highly resistant to some collections of *P. rubigo-vera tritici*, while it was highly susceptible to others. Thus in this way it could be divided into two groups. When the cultures were sown on another line, as for example Webster "C. I. 3780," it was found that the cultures of each group could be again segregated according to their reaction to Webster, and thus four groups were distinguished according to their reaction to both Malakoff and Webster. If instead of Webster another variety such as Mediterranean is used, four groups are still distinguished, but the cultures are not classified in the same way. It is evident that species, races, and forms are each groups delimited by the criteria employed. A change in the criteria, therefore, is likely to result in a regrouping.

RUST REACTION AS A MEANS OF CLASSIFICATION

Not only the rust parasites may be characterized by the reaction of species and varieties of their hosts, but such hosts often may be likewise identified and characterized by their reaction toward certain species and forms of the rusts, as has been noted by a number of investigators (Eriksson, 1895b; Ward, 1902c, 1903a; Klebahn, 1904a; Vavilov, 1913, 1914, 1919; Brierley, 1925; and others). In taxonomic studies of the rusts, unknown hosts are often identified by the rusts occurring on them. Arthur (1918b) decided that *Uredo circinata*, described by Schweinitz from Surinam on an unknown host is on a species of Stigmaphyllon, on account of a similarity to rusts on that genus. Many other instances of this nature have been recorded. Klebahn (1904a) reported establishing the identity of a willow through its reaction to *Melampsora ribesii-purpurea*. Stakman and Levine (Aamodt & Levine, 1925) have been able to distinguish *Festuca elatior* L. from *Festuca pratensis* Huds. by means of differences in reaction to *Puccinia graminis phlei-pratensis*. Vavilov (1913) was able to distinguish a number of varieties of oats and wheat by means of their rust reaction and was able to detect errors in the classification of several varieties of wheat and barley. Using physiologic forms of *P. graminis tritici*, Aamodt and Levine (1925) compared the reaction of the emmer developed by Love and Craig from a cross between *Triticum vulgare* and *T. durum* with the reaction of the natural wild emmer, *T. dicoccum dicoccoides*, and found a resemblance in reaction. They conclude that this "furnishes additional proof of their similarity, and supports the view of Love and Craig regarding the probable origin of natural wild emmer." Johnston and Bower (1924)

have used a form of *P. graminis tritici* to which Kanred is resistant to determine the purity of Kanred seed wheat offered for certification and have pointed out the possibility of likewise distinguishing other varieties by the use of the proper physiologic forms of rusts.

There is no reagent more delicate than living organisms (Dufrénoy, 1919), since they can make apparent those biochemic and biologic characters which are peculiar to each group of individuals. Parasites, therefore, can become such sensitive biologic reagents as to permit the distinction between groups otherwise indistinguishable.

Intimate relationship tested by rusts. — It has been recognized for a long time, that the rusts tend to occur on more or less closely related hosts. As has been noted, the various species, races and forms of rusts show considerable differences in their degrees of specialization. Ward (1902c, 1903a) found a correlation between the grouping of species of Bromus according to susceptibility to *Puccinia rubigo-vera bromi* and the grouping as obtained in other ways. Vavilov (1913, 1914, 1919) has used races of *P. rubigo-vera tritici*, *P. glumarum*, *P. graminis*, *P. anomala*, and *P. coronata* in extensive studies of varieties of wheat, barley and oats in order to determine relationship. He states that the conclusions reached in this way agree closely with those reached by Zade,[1] using serum tests to determine relationships in the cereals. He found that all the varieties of *Triticum monococcum* were resistant to *P. rubigo-vera tritici*, *P. glumarum* and *P. graminis*. *Triticum polonicum*, *T. turgidum* and *T. durum* were found to contain a large number of varieties resistant to *P. rubigo-vera tritici* and *P. glumarum*, while *Triticum compactum* and *T. vulgare* were for the most part susceptible. This he considered is in agreement with the evidence obtained in other ways. *Triticum monococcum* occupies a separate place among the wheats, not giving fertile hybrids with the other seven species. *Triticum polonicum*, *T. turgidum* and *T. durum* being genetically nearly allied, give fertile hybrids when crossed, but are genetically distinct from *T. compactum* and *T. vulgare* with which they give either sterile or partly fertile hybrids when crossed. In oats Vavilov found that the immune varieties belonged to *Avena brevis* and *A. strigosa*, which cannot be crossed with the susceptible species, *A. sativa*. A race of *A. strigosa* susceptible to rust was shown to be genetically different from the other races of the species and could be crossed with *A. sativa*. Varieties of *A. byzantina* immune to rust are considered phylogenetically distinct from susceptible oats. Naked bar-

[1] Zade, M. Serologische Studien an Leguminoseen und Gramineen. Zeits. Pflanzensuchten. **2** : 101–151. 1914.

leys are considered distinct from the bearded varieties in their phylogeny, and this, it is believed, explains their lesser susceptibility to rust. He also considers that since all varieties of barley are easily crossed, no sharp differences in immunity to rust are to be expected. Vavilov concludes that as a rule marked immunity of a variety is connected with a distinct genetic place among other varieties. Eriksson and Henning (1896), however, believe that the genetic position of wheat varieties can not be determined by the use of *P. glumarum.*

Although the reaction to rusts may be used to furnish some evidence of relationship, yet until more is known concerning the nature of the factors responsible for resistance and suescptibility, too much weight should not be given to such evidence. While the grouping of species and varieties according to their reaction to a certain rust may, in some cases, agree closely with their grouping as determined by morphologic and genetic evidence, as has been shown by Vavilov, the grouping according to their reaction to another rust may differ considerably. Thus Hungerford and Owens (1923) found that, in addition to a number of varieties of Triticum, 47 species in 7 genera of wild grasses are susceptible to *P. glumarum tritici* while a number of varieties of Triticum are resistant. Similar situations occur in other weakly specialized rusts such as *P. graminis* and *P. coronata.* It is obvious in these species that grouping according to similarity in rust reaction is not in agreement with other evidence. It has already been shown (Table 16) that two strains of Turkey wheat (Malakoff "C. I. 4898," and Turkey "47") react the same to physiologic forms of *P. rubigo-vera tritici* while other strains of Turkey react differently (Mains & Jackson, 1926), and also that a strain of the variety Norka ("C. I. 4377") reacts the same as the two Turkey strains (Malakoff "C. I. 4898," and Turkey "47"). Turkey is a white-chaffed winter wheat while Norka is a brown-chaffed spring wheat. Based on reaction to rust, Norka and two of the Turkey strains would be grouped together while the other Turkey strains would be placed in a separate group. Yet upon other characters, the Turkey strains are grouped together while Norka is distinct from them.

Correlation of susceptibility and immunity. — Vavilov (1919), as the result of his studies on the specialization of a number of parasitic fungi, including the rusts *Puccinia graminis, P. coronata, P. anomala, P. glumarum,* and *P. rubigo-vera tritici,* concludes that prevalence of resistant varieties in a species is correlated with the degree of specialization of the parasites. Species such as *P. rubigo-vera tritici, P. anomala, P. glumarum tritici* and *P. glumarum hordei* are considered

as narrowly specialized, and he finds a considerable number of varieties immune to these rusts. *Puccinia coronata* is considered as medium in specialization, and although there are some varieties immune, yet most varieties of *Avena sativa* are given as susceptible. *P. graminis tritici* is considered as weakly specialized, and it is stated that on the whole all varieties of wheat are susceptible although some varieties of *T. durum*, *T. dicoccum*, and *T. monococcum* are comparatively less attacked. *P. graminis avenae* is considered as very weakly specialized, and it is stated that no variety of oats was found to be immune.

However, Stakman and Levine (1922) report several varieties of *Triticum vulgare*, *T. durum*, *T. dicoccum* and *T. monococcum* to be highly resistant or immune to one or more physiologic forms of *P. graminis tritici*. While Durrell and Parker (1920) from their studies concerning the comparative resistance of varieties of oats to crown and stem rust conclude that there are more varieties resistant to crown rust, *P. coronata*, than to stem rust, *P. graminis avenae*. Stakman, Levine and Bailey (1923) also report two oat varieties highly resistant to some physiologic forms of *P. graminis avenae*. As to *P. glumarum tritici* Hungerford and Owens (1923) have shown that it is not a narrowly specialized race, as Vavilov has listed it, but goes to 47 species in the genera Agropyron, Elymus, Bromus, Hystrix, Sitanion and Phalaris, besides species of the genus Triticum. The existence of large numbers of wheat varieties highly resistant or immune to this rust consequently does not agree with Vavilov's hypothesis. It apparently, therefore, does not necessarily follow that a weak specialization precludes the possibility of the existence of immune varieties in a species of the host.

Resistant varieties or strains have been found among a wide range of genera and species, which otherwise are susceptible to the rust occurring on them. Instances of this kind have been discovered in alfalfa (Mains, 1926b), apples (Giddings & Berg, 1915b; Reed & Crabill, 1915), beans (Fromme & Wingard, 1921), blackberries (Dodge, 1923c), carnations (Stewart, 1896; Mains, 1926b), chrysanthemums (Gibson, 1904), coffee (Butler, 1918a), cowpeas (Fromme, 1924), currants (Eriksson, 1898b; Spaulding & Gravatt, 1917), flax (Vavilov, 1919; Hart, 1926; Henry & Stakman, 1925), grapes (Shear, 1924), pines (Klebahn, 1924), plums (Ducomet, 1924), roses (Vavilov, 1919; Laubert, 1920), sunflowers (Spragg & Down, 1920), timothy (Barker & Hayes, 1924), and in various cereals and wild grasses (Biffen, 1907; Beauverie, 1924; Carleton, 1899; Crépin, 1923; Clark, Martin & Stakman, 1926; Durrell & Parker, 1920; Eriksson, 1895a; Foëx, 1924; Gassner, 1919; Hoerner,

1919; Hungerford & Owens, 1923; McAlpine, 1910; Mackie & Allen, 1924; Mains, 1926a, b; Mains & Jackson, 1926; Mains & Leighty, 1923; Melchers & Parker, 1922a; Parker, 1918; Reed, 1920; Schaffnit & Rump, 1923; Sorauer, 1909; Stakman & Levine, 1922; Stakman, Levine & Bailey, 1923; Stakman, Levine & Griffee, 1925; Vavilov, 1913, 1919; Waterhouse, 1923).

Resistance and immunity have been found to be inherited in a number of instances as simple factors. The above studies have indicated that resistance of different varieties is not always the same, and genetic studies of the hosts have further supported this by proving their inheritance as separate factors. From this point of view it appears that susceptibility to rust depends upon the presence of factors governing compatibility in both the host and rust (Fig. 135). Such factors may be found in some cases among most or all the individuals of a species in a wide range of hosts. In other cases they are restricted to a few varieties or even strains, while in still other cases, they may be found only in a restricted number of varieties or strains belonging to different species of several genera, while other varieties or strains of these same species may possess factors resulting in incompatibility. Other rusts requiring other conditions for development may find such in other host combinations.

As compatibility and incompatibility in many cases are not coincident with morphologic characters, it is to be expected that these factors will be found variously distributed among hosts thus classified. When in the course of evolutionary development factors responsible for susceptibility are distributed through a series of genera, the rusts with corresponding factors are able to develop upon species of those genera possessing such factors. But if genera or species arise that are immune, the rusts are excluded from such lines of hosts, unless a corresponding change occurs in the rusts. Under the former condition the rusts may be able to infect species in a number of genera while other species may be immune, as in the case of *P. graminis*. Where such factors have been developed in only one species the rusts are necessarily limited to that species, and if only part of the individuals of the species carry such factors, the rusts are necessarily limited to such individuals. When groups of individuals are isolated, homozygous for the factors governing compatibility and incompatibility, susceptible lines develop in the first instance and resistant lines in the second, *e.g.*, in *P. rubigo-vera tritici*. In the rusts also those factors responsible for compatibility may be inherited independently of morphologic characteristics by which the species are

delimited. Since compatibility may depend upon the presence of the proper combination of a number of different factors in both host and parasite, there exist possibilities of a large number of different lines in both hosts and parasites depending upon the occurrence of such factors in each. The possibilities are so numerous that it is not much wonder that a bewildering complexity of morphologic and physiologic groupings can be obtained.

NATURE OF RESISTANCE AND SUSCEPTIBILITY

Considerable attention has been devoted to the factors which are responsible for specialization. While the exact nature of the factors has been determined in only a few instances, some light has been thrown on the matter by various studies in cytology, genetics, morphology and physiology.

Cytologic evidence. — Various symptoms are manifested when plants are invaded by rusts (p. 232). Sometimes no macroscopic effect is evident following inoculation, and microscopic examination shows that no pathologic condition has resulted (de Bary, 1863a, 1887; Gibson, 1904). In such instances the germ-tube may not be able to enter the stoma, or if it enters, growth continues only for a short period, two to four days. The germ-tube in such cases does not send haustoria into the cells which it encounters, has no deleterious effect on them, and soon becomes shriveled and dead. Such plants are truly immune.

While sometimes no macroscopic effects are produced following inoculation, yet a microscopic study may show that infection has actually occurred. Occasionally the germ-tube enters through the stoma in the usual way, but when the developing haustoria come in contact with the host's protoplasm, both the cell of the invaded host and that of the mother-cell of the haustorium collapse (Allen, 1923a, b, 1926a). A similar situation may result when there is infection of resistant hosts by basidiospores (Klebahn, 1896). If the rust mycelium possesses enough vigor, it sends out more haustoria into the cells of the host, but these in turn die. In some instances death of the invaded cell does not occur immediately, and the haustorium probably obtains some food before death finally results. In such cases the life of the mycelium of the rust is prolonged and a larger number of cells are invaded and eventually killed, before the rust itself dies. Where the cells that are affected are few (6–24) no macroscopic effect is noticeable.

When the adjustment between the host and rust is better, the killing

of invaded cells is delayed and the rust mycelium develops more extensively before it finally dies (de Bary, 1863a; Marryat, 1907; Stakman, 1914a; Allen, 1923b, 1926a, 1927). In some instances not only the invaded cells but adjoining cells are killed, apparently by the outward diffusion of some toxic substance that causes plasmolysis in the surrounding tissue (Allen, 1927). With increase in the number of cells killed the effect can be noted macroscopically as flecks, or necrotic spots of various sizes. It would appear that the various types of resistance, classified by the extent of necrosis and size and number of uredinia, depend upon the amount of food which the rust is able to obtain from its host before the cells of the host are killed. Sometimes there may be a certain amount of readjustment between the rust and host, so that later invaded cells are not affected so rapidly, and may even be stimulated to some extent. The cells of the host beyond the infected area also may be seriously influenced, resulting in a ring of chlorotic tissue inclosing a "green island" (p. 305). The rust may grow out through this dying area, sometimes stimulating it to a temporary activity, and may develop somewhat in the newly invaded area. Although the rust in such cases may develop to an extent that it is able to sporulate, the uredinia are usually few and small.

From the above it is evident that the reactions of the host may be divided into three classes, (1) those in which the cells of the inoculated plant are not invaded, (2) those in which invasion takes place, and the death both of the cells of the host and of the rust follows with more or less rapidity, (3) those in which successful invasion takes place without any pronounced immediate necrotic effect. The last situation is usually classed as susceptible. The first two are not always distinguishable macroscopically and they oftentimes are not differentiated, the term "resistant" being used to describe both conditions. The term "immune" has also been used to cover both classes. Some investigators have restricted the term "immune" to cover all of those conditions in which sori are not formed (Stakman & Levine, 1922). So used, the term "immune" not only applies to plants in which the cells are not invaded, but also to those in which invasion occurs but death of the invaded cells and of the rust results before the latter is able to sporulate. If, however, the rust is able to produce small uredinia before the death of the invaded cells brings about a cessation of the development of the rust, the plants are classified as "resistant." It appears desirable to distinguish the condition in which cells are not invaded from that in which invasion occurs, even though the final elimination of the rust in both

cases is the same. It may be that the two conditions are brought about by quite different factors. Certainly if, as suggested by Stakman's term "hypersensitive," resistance is excessive susceptibility, it is further removed from the condition of non-invasion than is the condition implied in the term "susceptible." The condition, in which rusts are not able to invade the cells of inoculated plants, certainly deserves a distinctive term. Immunity as distinguished from resistance can be properly applied to this condition (Zimmermann, 1925). So far as possible the three classes listed above will here be denoted as (1) immune, (2) resistant, and (3) susceptible.

Genetic evidence. — In a number of genetic studies resistance was found to be inherited as a dominant character, as the resistance of rye to leaf rust, *Puccinia rubigo-vera secalis*, and also to stem rust, *P. graminis secalis* (Mains & Leighty, 1923; Mains, 1926b). The resistance of flax to *Melampsora lini* is inherited as a dominant character. In some crosses the ratio in the second generation (F_2) has been found to be 3 : 1, that is, three resistant to one susceptible, while in others it approximated 15 : 1 (Henry, 1926b). In crosses between Kanred and other varieties of common wheat the resistance of Kanred to certain physiologic forms of *Puccinia graminis* was found to be inherited in the ratio of three resistant to one susceptible (Melchers & Parker, 1922b; Aamodt, 1923). Similar results have been obtained in a cross between two varieties of durum wheat (Harrington & Aamodt, 1923). A similar ratio has been reported for the inheritance of resistance to *P. graminis* in oats (Garber, 1922; Griffee, 1922; Dietz, 1925) and also of *P. coronata* in oats (Davies & Jones, 1926). The resistance of several varieties of wheat to *P. rubigo-vera tritici* is inherited in a similar way according to Mains, Leighty and Johnston (1926). The same investigators, however, report that the resistance of other varieties of wheat to *P. rubigo-vera tritici* is a recessive character, the ratio in the second (F_2) generation being three susceptible to one resistant. Hayes, Stakman and Aamodt (1925) in their studies of a wheat cross have found that while the marked seedling resistance of one parent in the greenhouse to certain physiologic forms of *P. graminis tritici* is inherited as a simple dominant character, the moderate field resistance of the other parent was inherited as a recessive character in the ratio of 1 : 15, "indicating . . . the interaction of two genetic factors, both of which must be present in a homozygous condition to produce resistance." A cross between Kota "immune" and Marquis resistant to *P. graminis* "physiologic form 27," gave Hayes and Aamodt (1923) in the third (F_3) generation lines homo-

zygous for susceptibility, from which they conclude that there are "two independently inherited factors for immunity and resistance in the Kota and Marquis parents respectively, each factor allelomorphic and dominant to a factor for susceptibility." Somewhat similar results were obtained by Harrington (1925) in a cross between durum varieties. Resistance to *P. glumarum tritici*, according to Biffen (1905, 1907), is a simple recessive factor, the ratios in the F_2 generation being approximately one resistant to three susceptible. The genetic evidence in these studies indicates that frequently the resistance of the varieties studied is due either to a single genetic factor or else to a group of factors very closely linked together. Sometimes the factor or factors responsible for resistance are dominant and sometimes recessive, even to the same species of rust, indicating that such factors differ in their nature.

The combination of a number of factors may be necessary for the expression of resistance, as indicated by the results of studies with *P. glumarum tritici* (Nilsson-Ehle, 1911; Armstrong, 1922), with *P. graminis tritici* (Clark, 1925; Hayes, Stakman & Aamodt, 1925; Harrington, 1925), with *P. graminis avenae* (Dietz, 1925), and with *P. rubigo-vera tritici* (Mains, Leighty & Johnston, 1926).

Independent inheritance of resistance. — Not only may resistance to various rusts be separately inherited as has been shown for resistance of rye to *P. rubigo-vera secalis* and *P. graminis tritici* (Mains, 1926b), but resistance of various varieties of the same species to different physiologic forms of a rust may also be inherited separately. A cross between Mindum (*Triticum durum*), which is resistant to *P. graminis tritici* "physiologic form 1" and susceptible to "p. f. 19," and Marquis, which is susceptible to "p. f. 1" and resistant to "p. f. 19," has shown all combinations of resistance and susceptibility to the two physiologic forms among the second (F_2) generation (Puttick, 1921). A small proportion of the F_2 plants have shown a combination of the resistance of the parents to both physiologic forms. Similar results have been reported by other investigators (Harrington & Aamodt, 1923; Hayes & Aamodt, 1923; Hayes, Stakman & Aamodt, 1925; Harrington, 1925). Resistance of one wheat variety to a physiologic form of *P. rubigo-vera tritici* is inherited independently of the resistance of another variety to other physiologic forms, and the resistance of the two varieties may be combined in a homozygous condition in a definite proportion of the F_3 lines (Fig. 135), according to Mains, Leighty and Johnston (1926).

There is but little genetic evidence linking rust resistance with any

other character, remembering, however, that tests have only yet been made with a few characters. With wheat crosses and certain physiologic forms of *P. graminis tritici* no linkage has been found between resistance and seed color (Harrington & Aamodt, 1923; Harrington, 1925), between the habit of winter growth and spring growth (Aamodt, 1923), or

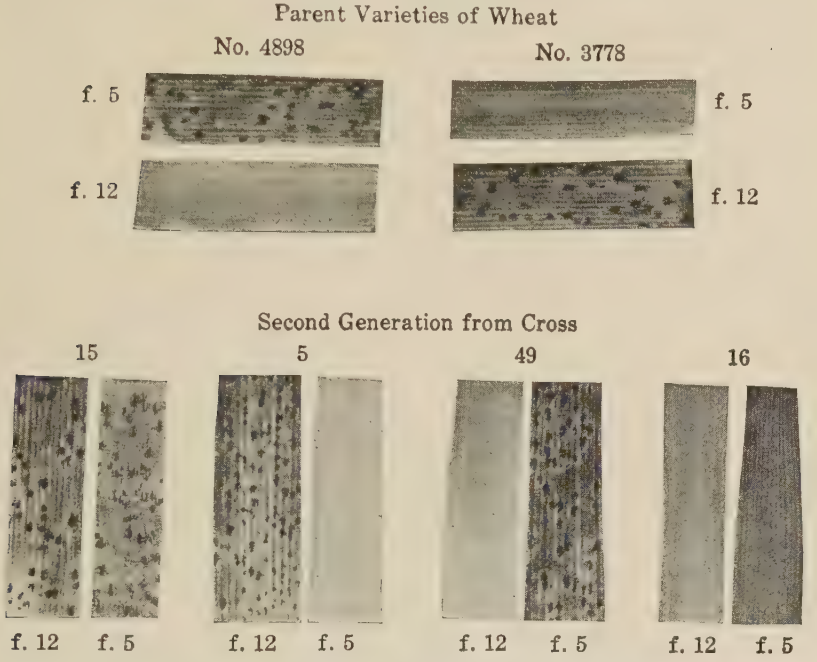


FIG. 135. — Inheritance of resistance to *Puccinia rubigo-vera tritici* in two varieties of wheat: Malakoff no. 4898 (which had been shown to be resistant to form 12 of the rust and susceptible to f. 5) was crossed with no. 3778 of another variety (which had been shown to be resistant to f. 5 of the rust but not to f. 12), the resulting seed sown and the plants allowed to self-fertilize. There were 85 plants produced in the 2nd generation from the cross, and when tested with the two forms o rust gave 15 plants susceptible to both forms, 5 susceptible to f. 12 and resistant to f. 5, 49 resistant to f. 12 and susceptible to f. 5, and 16 resistant to both forms of rust. (For details see Mains, Leighty & Johnston, 1926, p. 959.)

between factors governing presence of awns and seed length (Hayes & Aamodt, 1923). Nevertheless, as a result of studies of the inheritance of resistance to *P. graminis tritici* in crosses of varieties of common wheats with varieties of durums and emmers there is an indication of linkage between durum or emmer characters and rust resistance (Hayes, Parker & Kurtzweil, 1920; Sax, 1923; Hayes, Stakman & Aamodt, 1925; Thompson, 1925).

In crosses between emmers or durums which possess 14 haploid chromosomes and varieties of common wheat with 21 chromosomes considerable sterility results in the progenies, possibly due to the "unbalanced numerical relations of the chromosomes" (Sax, 1923). The ultimate homozygous fertile segregates tend to have either 14 or 21 chromosomes. Sax concludes that "in view of the fact that the morphologic and physiologic characters of the *vulgare* wheats are associated with the seven additional chromosomes, it is improbable that the desirable characters of the emmer and *vulgare* wheats can be combined in homozygous fertile segregates." While Hayes, Stakman and Aamodt (1925) find that there is linkage between *vulgare* characters and susceptibility in crosses between resistant durums and susceptible commons, they consider that this linkage is not absolute and believe that there is some hope of developing a *vulgare* type with the resistance of the durums.

Combined resistance to parasites. — Various opinions have been held concerning the relationship of resistance to rust and resistance to other parasites. It has been stated by Vavilov (1919) that instead of varieties resistant to one parasite being susceptible to another as usually supposed, there is a definite connection of combined resistance in varieties of wheat to brown rust, yellow rust, black rust, and mildew, in that all varieties resistant to brown rust, black rust and mildew are resistant to yellow rust. It has been stated (Sax, 1923) that wheats resistant to rust are also resistant to bunt. It is found that when applied to specific cases generalities do not always hold. Thus it has been found (Mains, 1926b) that resistance to *P. rubigo-vera secalis*, *P. graminis secalis* and *Erysiphe graminis secalis* is inherited separately for each parasite, and plants have been obtained showing different combinations, such as resistance to all three, resistance to two and susceptibility to one, resistance to one and susceptibility to two, and susceptibility to all three. From a cross between the wheat varieties "Egyptian No. 3," resistant to *P. graminis* and susceptible to *P. glumarum*, and "Nut Cut" susceptible to *P. graminis* and resistant to *P. glumarum*, Dawson (1921) obtained a selection resistant to both rusts. The extensive studies which are being made concerning the reaction of varieties to various parasites indicate in the results so far obtained that in many cases there is no correlation between the reactions to the various parasites (Jenkin & Sampson, 1921; Mains, 1926b). Some varieties of wheat for example, which are resistant to leaf rust are susceptible to bunt, loose smut, stem rust, powdery mildew, etc.,

while other varieties are resistant to physiologic forms of both leaf rust and stem rust, to leaf rust and bunt, to leaf rust and powdery mildew, etc. While resistance to several parasites may sometimes be due to the same factors, at other times the factors responsible apparently are different. The genetic results afford additional evidence that often the resistance of different varieties to the same species of rust is due to different causes. The differences in manner of inheritance, the synthesis of lines combining the resistance of several varieties to different physiologic forms, indicate that a number of diverse factors may bring about the same or similar types of resistance. The evidence so far obtained does not, however, give any idea of the nature of the responsible factors.

Reaction of grafts. — The question of the effect of the stock on grafts has received some study. While Klebahn (1904a) states that *Ribes grossularia* which is ordinarily resistant to *Cronartium ribicola*, when grafted on *Ribes aureum* can be successfully infected, yet Schellenberg (1923), concludes from his observations that the stock does not change the reaction of the graft. It was noted by Blaringhem (1924) that a variegated variety of *Lavatera arborea* was only weakly infected by *Puccinia malvacearum*, but when grafted on a green variety it was as vigorously infected as was the green variety. Zimmermann (1925) has suggested that the difference here noted was probably due to increased vigor in development of the graft. In studies of the reaction of pomaceous grafts to Gymnosporangium no effect of the stocks upon the grafts has been noticed (Fischer, 1912; Sahli, 1916). Shoots of a susceptible variety of chrysanthemum when grafted upon a resistant variety were found to be as susceptible to *Puccinia* (*Uredo*) *chrysanthemi*, as if growing on their own roots (Gibson, 1904).

Reaction of chimeras. — Fischer (1913) and Sahli (1916) have carried out rather extensive experiments with periclinal chimeras. In one of these, the central tissue was derived from Crataegus while the epidermis was derived from Mespilus. To *Gymnosporangium clavariaeforme* Mespilus is highly resistant and Crataegus susceptible, yet in the chimera the Crataegus tissue was found to be seemingly highly resistant. This is explained by the protection afforded by the Mespilus epidermis through which the germ-tubes of the basidiospores apparently were not able to penetrate. Crataegus is susceptible to *Gymnosporangium confusum* while Mespilus is only moderately susceptible. The infected chimera showed a longer incubation period than usual with Crataegus. In another chimera, in which there was a layer of Mespilus two cells

thick, the incubation period was still longer, but sporulation finally resulted. Apparently in these instances, the rust passed through the Mespilus cells but growth of the hyphae was slower than in the more favorable cells of Crataegus. Once in the Crataegus tissue, vigorous growth of the rust occurred.

This evidence indicates that the reactions of the tissues involved in these grafts are dependent upon genetic differences, which are not changed when combined in the same plant. While there is an interchange of substances between the tissues, such substances do not materially modify the original reaction to the parasite. It appears, therefore, that the substances responsible for resistance and susceptibility should be sought in the processes within the living cell.

Morphologic evidence. — The earlier attempts to explain resistance and immunity were largely through morphologic characters, especially such as would prevent the entrance of the rust or limit its development. Later researches have shown that morphologic hindrances to infection are of a special and limited nature.

Since contact with water is one of the requirements for spore germination in many species of rusts, conditions unfavorable for the collection of water on the surface of plants may limit or prevent infection. It has been said that resistant wheats possess narrow, erect leaves with waxy bloom, from which water tends to roll off (Bolley, 1889a; Cobb, 1892; Farrer, 1898). The greater difficulty experienced in infecting older wheat plants as compared with seedlings may be due to the fact that the former do not as readily retain a film of water as the latter (Puttick, 1921).

Since the germ-tubes of aeciospores and urediniospores enter plants through stomata, such openings into the intercellular spaces are necessary before infection can occur, and tissues free from such openings should be immune to rust infection. A correlation has been found between the number and size of stomata and rust infection (Norton, 1913; Appel, 1915; Doran, 1921; Allen, 1921, 1923a). The varieties of snapdragon, which show most rust, possess the largest number of stomata per unit of area (Doran, 1921). About 90 per cent of the uredinial germ-tubes of *P. graminis tritici* are unable to enter Kanred wheat, the stomata being smaller than usual, and the naturally small stomatal slit is often further narrowed following contact with the appressorium (Allen, 1921, 1923a).

The degree of hairiness of resistant wheat varieties has been found to be insufficient to explain their resistance to rust (Cobb, 1892), yet a

tomentose covering of a thickness sufficient to prevent the germ-tubes of the rust reaching the stomata undoubtedly may in some cases prevent rust infection.

The basidiospore usually forms a very slender, pointed beak, which is forced through the cuticle of the host (p. 229). The penetration appears to be independent of any enzymatic action, and in some instances, *e.g.*, *Puccinia graminis*, if not in all others, may be due to mechanical action (Waterhouse, 1921). The leverage is made possible by the gelatinization of the surface of the germinating basidiospore, which enables the spore to adhere firmly to the cuticle (Fig. 131).

The penetration of the germ-tubes of the basidiospores into epidermal cells may possibly be prevented by the thickness or strength of walls of such cells, and this may also be true of the penetration of haustoria. In old needles of *Pinus virginiana* the germ-tubes of the basidiospores of *Gallowaya pinicola* are unable to force their way into the tissue, while in young needles infection readily occurs (Galloway, 1896). In a study of the resistance of Berberis and Mahonia to infection a certain amount of correlation has been found between basidiosporic infection and the thickness of outer walls of the epidermis and of their resistance to puncture. A delicate mechanical device was used to test the resistance to puncture (Melander & Craigie, 1927). The difficulty of infecting old leaves with basidiospores, in the opinion of Klebahn (1904a), is due to the greater resistance of the epidermal cell-walls to penetration by germ-tubes of the basidiospores. It has been found that wheat and other cereals grown in solutions deficient in silicic acid suffer severely from rust (Palladin, 1923), and it may be that cell-walls impregnated with silica play an important rôle in protection against parasites.

A correlation between the thickness of the epidermal cells and rust development in certain wheat varieties has also been noted (Cobb, 1892), which is doubtless due to the toughness of the epidermis. This condition prevents rupturing by the sori and restricts sporulation and dispersal of the spores.

Several investigators have found that the mycelia of some rusts may be limited in their development by the morphologic nature of host-tissues. *Puccinia fraxinata* and *P. distichlidis* are two unlike rusts occurring on Spartina, the first forming its sori adjoining the collenchyma of the sheaths and upper part of the blade, the second in the parenchyma of the under part of the blade (Arthur, 1902b, 1907–27). The mycelium of *P. graminis* is restricted to the chlorophyll-bearing parenchyma and does not develop in the collenchyma (Sappin-Trouffy, 1896; Cobb,

1892; Hursh, 1924). In certain wheat varieties the parenchyma is only slightly developed and is bordered by a large amount of collenchyma with a corresponding restriction in the development of the rust.

It is possible that in some instances morphologic characters of the host may secure immunity, or else afford marked hindrance to infection. It seems probable that in the presence of a small amount of inoculum, plants affording morphologic hindrances to infection will not develop the maximum infection rapidly, and in seasons unfavorable for rust they may never reach the maximum amount. Extensive investigations, however, have shown that frequently resistance can not be explained by morphologic conditions (Ward, 1902c; Eriksson & Henning, 1896; Biffen, 1912; Vavilov, 1913, 1919; Garber, 1922; Allen, 1923a; Hursh, 1924; Zimmermann, 1925).

Physiologic evidence. — Considerable evidence has accumulated indicating that resistance for the most part is due to physiologic reactions between the rust and the inoculated plant.

Immunity due to the inhibition of spore germination has been studied by Robinson (1914), who states that germination of the basidiospores of *Puccinia malvacearum* is for the most part inhibited when placed on the leaves of *Primula vuglaris*, garden geranium (Pelargonium) and *Eucalyptus globulus*. Glandular secretions in these cases had a definite toxic effect as shown by the contorted germ-tubes of the few spores that germinated. The presence of leaves of *Althaea rosea, Ranunculus ficaria*, etc., had no effect. It was found that basidiospores germinate as readily on leaves of potato as on those of Althaea. In both cases the germ-tubes become swollen and appressed to the epidermis, but while the germ-tubes are able to penetrate the epidermis of Althaea, there was no sign of penetration in the case of potato. The spore germination of *Puccinia rubigo-vera bromi* tested in cold water extracts of macerated leaves of both susceptible and resistant species of Bromus exhibit no differences (Ward, 1902c). Urediniospores of *P. graminis tritici* germinate equally well on resistant and on susceptible varieties of wheat (Allen, 1923a, 1927; Hursh, 1924). There seems to be little evidence that spore germination is prevented by either resistant or immune plants.

It has been suggested that the germ-tubes of the rusts may be influenced chemotropically by substances in living plants (p. 228). It is conceivable that sometimes immunity may be due to absence of substances or to the presence of compounds which produce a negative chemotropic response. However, it has long been known (de Bary, 1863a, p. 84; Gibson, 1904) that the germ-tubes enter the stomata of

plants which are completely immune, indicating that if chemotropic responses affect the entry of germ-tubes, the substances responsible are generally present in all living plants. Such being the case, immunity cannot in general be explained by chemotropism.

The uredinial and aecial germ-tubes can penetrate into the intercellular spaces but the haustoria do not enter the cells of completely immune plants (p. 263). Various suggestions have been offered to explain such conditions. If the haustoria of the rusts are able to penetrate cells by enzymatic action, it may be that the chemical nature of cell-walls and the ability of the rust to secrete the appropriate enzyme may in some cases determine immunity. On the other hand the cells of immune plants may excrete substances toxic to the rust, producing the death of the hyphae before the rust can penetrate into cells of the surrounding tissue. It has been found that hyphae in the intercellular spaces of immune plants die sooner than germ-tubes outside of such plants, which may be due not so much to starvation as to some poisonous substance emitted by the cells of the invaded plant (Gibson, 1904). There are, however, few data upon which to base conclusions regarding this question.

When the rust is able to penetrate the cell-walls of the invaded plant and send haustoria into the cells, a reaction may develop resulting both in the death of the cell and that of the rust. The degree of resistance apparently depends upon the degree of incompatibility and the rapidity with which death results to both the host-cells and the rust parasite. Various explanations have been offered to account for this type of resistance. A correlation has been noted between high acidity and resistance (Comes, 1913; Kirchner, 1916; Zimmermann, 1925). On the other hand, other investigators have not been able to find any such correlation (Vavilov, 1919; Hurd, 1923; Arrhenius, 1924; Hursh, 1924). It is possible that in some cases acidity either may be a factor in promoting resistance or may be associated with the factors responsible for resistance.

Osmotic pressure may play a part in limiting infection. If the osmotic pressure of the cells of the invaded plant is higher than that of the rust, infection can not take place without a readjustment. It has been observed (Allen, 1923a) that cells of the susceptible Baart wheat are plasmolyzed by killing solutions, while the mycelium of *P. graminis* under the same conditions becomes well fixed, indicating for the latter a higher osmotic pressure. It was also found that although uninfected cells of the resistant Kanred variety were plasmolyzed, invaded cells

remained turgid while the haustoria and haustorium mother-cells were plasmolyzed, possibly indicating an increase in osmotic pressure of the infected cells. As the result of freezing-point and refractometric determinations of expressed sap of a number of wheat varieties that showed different degrees of susceptibility to *P. graminis*, Hursh (1924) concluded that there was no correlation between the amount of solids in the cell-sap and rust resistance. According to Zimmermann (1925), Pantanelli (1921) reached similar conclusions.

Various investigators have discussed toxins and antitoxins in relation to resistance. The resistance of some varieties of wheat "would seem to be explicable at present only by the toxin or enzyme theory" (Stakman, 1914a; Allen, 1927). That enzymes and toxins on the part of the rust and antitoxins and other enzymes of the host must be factors in determining susceptibility and resistance is the opinion of Ward (1905). As the result of cytologic studies Gibson (1904), Marryat (1907), and Allen (1923a) conclude that resistance in the cases studied is probably due to the production of toxins. The poisonous substances may be emitted by cells of immune plants, killing the rust hyphae before such cells are invaded (Gibson, 1904), or such substances are not evident in resistant plants until after their cells have been invaded by the haustoria (Allen, 1923a). On the other hand the toxic substance may be emitted by the fungus (Allen, 1923b, 1926a), and this substance may be an enzyme of the nature of a pectinase (Allen, 1927). As the result of studies on the effect of tannin on the spore germination of several rusts as well as other fungi, it has been suggested that tannin may possibly be responsible for the resistance of plants to parasites (Cook & Taubenhaus, 1911).

Several investigators have been unable to find any experimental evidence of toxins. Ward (1902c) sought to discover whether there might be some substance in the cell-sap of resistant plants which prevented the growth of rusts. He tried germinating urediniospores of *P. rubigo-vera bromi* in cold water extracts of leaves of both susceptible and resistant species of Bromus, and found that the spores germinated equally well in both. He points out, however, that it can hardly be supposed that the cell contents thus extracted are in the normal condition in which they exist in the living cell. Leach (1919) made extracts of infected wheat plants of a series of varieties showing different types of resistance and susceptibility to *P. graminis tritici* and found no correlation between the germination of urediniospores in such solutions and the reactions of the hosts. He concludes that there is no evidence

of a toxic substance secreted by resistant hosts in the cases studied. Such toxins, however, may be unstable compounds, and during extraction may change over into stable compounds which are without toxic properties, or they may be active only in the nascent condition in the living host (Zimmermann, 1925).

The statement that resistance is caused by toxins implies that some compound or compounds are responsible for a detrimental effect, but does not indicate the chemical nature of such compounds. There are various ways in which the reactions known to occur in resistant plants might be brought about by toxins, some of which have been discussed by Zimmermann (1925). It may be that certain compounds are excreted by a rust into the infected cells. In susceptible plants such substances may not disturb the metabolism of the invaded cell, possibly on account of identity with compounds developed by the host. In resistant plants with different metabolic reactions the same compounds may initiate radical changes interfering with its physiologic functions. Such substances may even mildly stimulate the cells of susceptible hosts producing an increased metabolic activity and resulting in an increased production of nutriments with resulting luxuriance of the parasite. In resistant plants there may be an overstimulation with an overthrowing of the metabolic balance resulting in the death of the invaded cells. One would then have the rather anomalous situation that the resistant plants would be more susceptible than susceptible plants, a situation suggested by Stakman's use of the term "hypersensitive" to describe the necrotic condition found in certain types of resistance. Zimmermann states that to explain immunity along this line, it would be necessary to assume that the toxin was without effect in immune plants, or that there is no exchange of materials between host and parasite, or that the fungus is not stimulated to secrete the toxin by such plants.

The death of haustoria in resistant plants may result from the production of an antitoxin in an attempt to neutralize the toxin from the rusts, or it may be that the protein compounds developed in the dying cells of resistant hosts are toxic to the rust, or that too great an osmotic concentration of soluble compounds or too great an acidity develops through the breaking down of the complex organic compounds of the dying cells. On the other hand, it may result through starvation since the reduced metabolism of dying cells probably results in a decrease in food production and dead cells cease to provide the food materials necessary for rust development. This, however, is nearly all supposition. There is no available evidence, such as has been accumulated in

animal pathology. Toxins and antitoxins have not been extracted, and the deductions have been largely drawn from the appearance of infected cells in the course of cytologic studies.

The rusts may be restricted to certain hosts by their food requirements. A higher sugar content has been found in certain susceptible varieties than in resistant (Kirchner, 1916; Pantanelli, 1921). A number of investigators have suggested that the rusts are dependent upon specific organic compounds that are to be found only in living plants. Proteins of definite structure are possibly factors in the specialization of the rusts (Zimmermann, 1925). As evidence in support of this opinion there is offered the positive serodiagnostic reaction, *fide* Wendelstadt and Fellner, obtained between *Impatiens balsamina* and *Tropaeolum minus*, both susceptible hosts for *Cronartium asclepiadeum*. The parallelism noted between the genetic relationship of various wheats and of various oats as determined by susceptibility to rusts (Vavilov, 1914) and the results of serodiagnostic studies (*fide* Zade) points in the same direction. That protoplasm is not directly utilized is indicated by the observation that cells full of protoplasm are not invaded, infection occurring only after they have become vacuolated (Tischler, 1911). It is suggested (Fromme, 1913) that the rusts may depend upon transition products in photosynthesis. However, it is probably not the stable carbohydrates or proteins that are essential, but some transitory or nascent compound developed during the synthesis of complex organic substances, or certain isomers of such compounds (Mains, 1917; Leach, 1919). In support of the idea that there is a "specificity of food requirement on the part of the fungus and a specificity of food production on the part of the host" Leach points out that it is possible to divide the type-hosts of the physiologic races of *P. graminis* into two distinct groups on the basis of starch peculiarities (Reichert, 1913), which will correspond with the classification into biologic races on the basis of parasitism (Stakman & Piemeisel, 1917). He also suggests that the necrotic effect noted in many resistant varieties may be due to excessive production of enzymes when suitable food is not readily available, and that such an excess of enzymes results in a toxic action on the protoplasm of the host. The observation, that in susceptible hosts necrosis is produced in infected areas when the host is so treated as to produce starvation of the rust (Ward, 1905), supports this opinion.

On the other hand the starvation theory evidently can not always explain the situation in resistant plants, as the germ-tubes of spores on the surface of immune plants have been found to be alive and unshrunken,

while those which had penetrated into the leaf were shriveled and empty, indicating a deleterious effect from some substance emitted by the cells (Gibson, 1904). "There seems little room for the 'starvation' theory of immunity" (Allen, 1923a), for "at every point of entry into a host-cell the fungus is either killed back or driven back for a short distance. When the reaction of the host is somewhat different, the fungus makes a haustorium and it evidently extracts food from the host — enough at least to let it grow to new cells — and there is no evidence that this food is of an unsuitable nature. To be sure the fungus sooner or later exhausts itself in these unsuccessful attempts to enter into food relations with the host, but the observations recorded here suggest that in this case at least, the failure of the fungus is due not so much to lack of proper food in the host as to a specific reaction set up there which destroys the fungus."

Variety and combination of factors. — It is evident from the literature that there is little positive evidence concerning the nature of the factors responsible for immunity, resistance, and susceptibility to rusts. In most cases attempts have been made to explain all resistance by some one characteristic or other, and when such explanations have not been found to agree with the results of other experiments, there has been a tendency to exclude such factors as possibilities. It is evident, however, both from the results of studies in pathology and in genetics, that resistance and susceptibility even to the same species of rust may be produced by a number of factors and these may be quite different in their nature.

STABILITY OF REACTION

Since specialization involves the reaction of the rust on the one hand and the reaction of the inoculated plant on the other, it follows that the relationship of the two organisms will vary if the reaction of either or both of them changes.

Rust stability. — The question whether specialized races or forms of the rusts may change their pathogenicity and extend their range of hosts has been studied both from the sporophytic side and the gametophytic side of the rust. By employing urediniospores or teliospores it has been claimed that a change of resistance could be brought about by means of certain "bridging species" of the hosts (Ward, 1903a).

A rust developed upon a "bridging species" was believed to acquire the ability successfully to infect species which were previously resistant to it. A number of species of Bromus have been designated as "bridging

hosts" for two or more races of *Puccinia rubigo-vera bromi* (Ward, 1903a), and *Helianthus annuus* has been selected as a "bridging host" for three races of *P. helianthi* (Arthur, 1905a), yet a careful analysis of the published data does not show that spores of known parentage taken from a "bridging host" were actually able to infect plants which were resistant to the same strain when not passed through the "bridging host."

In a similar way it has been thought that barley is a "bridging host" for *P. graminis* between wheat and oats (Freeman & Johnson, 1911), and that *P. graminis phlei-pratensis* can be transferred from Phleum to barley by means of *Avena sativa* or *Festuca elatior*, and to wheat by means of *Festuca elatior* or *Dactylis glomerata* (Johnson, 1911c). However, numerous experiments by other persons have failed to duplicate these results (Stakman, 1914b; Stakman & Jensen, 1915; Stakman & Piemeisel, 1917; Stakman, Parker & Piemeisel, 1918).

Hybrids between susceptible and resistant hosts are said by Evans (1911) to act as "bridging hosts." In a cross between a variety of wheat, Wol Koron, susceptible to *P. graminis* and a resistant variety, Bob's Rust Proof, the hybrid was more susceptible than the susceptible parent, and while the rust taken from the susceptible parent gave only slight infection on the resistant parent yet from the hybrid it gave a moderate infection.

On the contrary crosses between varieties of wheat susceptible and resistant to *P. glumarum*, made by Biffen (1912) showed no evidence of such "bridging" in the first generation, as resistant varieties in close proximity to F_1 plants remained resistant throughout eight seasons. He also points out that the close approximation of a 3 : 1 ratio would be impossible if resistant plants could become rusted from heterozygous individuals. Crosses made by Stakman, Parker and Piemeisel (1918) between Haynes Bluestem and Kubanka, Marquis and Emmer, Marquis and Kubanka, and tested with *P. graminis*, gave no evidence of changing the pathogenicity. The resistant parents, Kubanka and Emmer, showed the same resistance to the rust from the hybrids as from the original stock cultures. They conclude that "there seems no basis from the facts now at hand for the fear expressed by Pole Evans (1911) that these hybrids once produced will not only gradually lose their own power to resist attacks of the rust, but will also give the parasite new infection capabilities, enabling it to cause greater injury to susceptible varieties, and even to attack previously resistant varieties."

An attempt has been made to increase the virulence of a number of races of *P. graminis* by repeatedly sowing them upon uncongenial hosts

(Stakman, Piemeisel & Levine, 1918). It was possible in this way to secure a limited infection and some sporulation, and by resowing the spores so obtained to maintain the cultures through several generations. But there was generally a decrease in the number and size of the uredinia, until finally the cultures died out.

The preceding account has dealt with the sporophytic phase of the several rusts. The gametophytic phase has received no less attention, and studies have been carried on in much the same manner.

The aeciospores from *Berberis vulgaris*, which were grown by infection from *Agrostis alba*, were found successfully to infect *Hordeum vulgare* and *Triticum vulgare*, species unfavorable for *P. graminis agrostidis* (Arthur, 1907, 1908a, 1910b). From this and similar results Arthur (1910b) concludes that "in the aecial stage racial strains play no part, and the barberry acts as a 'bridging host' between each and every other gramineous host." After the same manner *P. coronata* has been successfully transferred from *Avena sativa* through its aecial stage on Rhamnus to *Holcus lanatus* and *Calamagrostis canadensis*, both the latter species showing resistance to the rust when transferred directly from *Avena sativa*. *P. coronata* will also pass from *Calamagrostis canadensis* to *Avena sativa* and from *Festuca elatior* to a series of species by way of the aecial host (Dietz, 1926a).

On the other hand extensive experiments with *P. graminis*, using teliospores from a large number of different grasses, have given no pronounced changes in the parasitic capabilities of the races as the result of its development on the common aecial host, *Berberis vulgaris*, when conducted in Sweden (Eriksson, 1894, 1902), Russia (Jaczewski, 1910), or the United States (Stakman, 1914a; Stakman, Piemeisel & Levine, 1918).

A number of examples of apparent "bridging," when analyzed, have proved to be due to mixed cultures. A culture of *P. graminis* taken from *Agropyron repens*, which had been found to infect rye and not wheat, and therefore presumably *P. graminis secalis*, was grown on barley, and from the barley, gave infection both on rye and wheat. This by itself indicated that *P. graminis secalis* had been changed by means of barley so that it was able successfully to infect wheat. Further cultures revealed, however, that a small amount of *P. graminis tritici* occurred in the original collection, which was able to develop spores only to a slight extent on *Agropyron repens*, yet on barley, a host favorable to both *tritici* and *secalis*, it developed spores abundantly. When the mixture was sown both on rye and wheat good infection occurred

on both hosts, although the original inoculation from *Agropyron repens* gave no indication of infection on wheat (Stakman, Piemeisel & Levine, 1918).

It has been suggested that the aecial stage may reinvigorate the rust, and result in a more robust development than when the rust is derived from urediniospores (Arthur, 1903b; Bolley & Pritchard, 1906). In testing this suggestion it was found that a rust after being grown continuously in the uredinial stage gave as vigorous response as the same form grown directly from aecia (Freeman & Johnson, 1911; Stakman, 1914a; Stakman, Piemeisel & Levine, 1918).

The opposite possibility to that of extension of pathogenicity, as outlined in the preceding paragraphs, that is, a change in pathogenicity to restrict the range of hosts, has also received some attention.

It has been suggested that races may have arisen through long association of the rust with given hosts (Magnus, 1894), and that in this manner from originally plurivorous rusts races may have gradually evolved, facilitated by differences in the prevalence of certain of their hosts in restricted localities (Dietel, 1899). This possibility has been tested by Klebahn (1904a) for his *P. smilacearum-digraphidis typica*, a race of *P. sessilis*. All the races of this species produce their telia on *Phalaris arundinacea*, and are distinguished by their aecial hosts. Klebahn's culture originally infected *Polygonatum multiflorum*, *Convallaria majalis* and *Majanthemum bifolium* vigorously, and *Paris quadrifolia* slightly. After ten generations of the aecia on *Polygonatum multiflorum* it was found that only *P. multiflorum* was infected vigorously, *Majanthemum bifolium* moderately, *Convallaria majalis* slightly, and *Paris quadrifolia* not at all. Although it appears from this series of studies extending over ten years that a restriction in pathogenicity had been produced, yet the question may still be raised, as in some of the preceding cases, whether the original culture was not begun with a mixture of races, and that the result was unwittingly attained by elimination of certain of the races, instead of by a change in pathogenicity.

Possibility of hybrids or mutations. — The rusts have generally been considered homothallic, and without much likelihood of variation due to biparental origin. The establishment of heterothallism for certain species of the Ascomycetes, Basidiomycetes, and the Algae, has brought the question into the foreground for the rusts (pp. 80, 94). It is possible that during the formation of cells with conjugate nuclei in the sporophyte the two nuclei may be derived from independent

sources, and in their ultimate fusion and maturation may unite their hereditary traits in accordance with the laws that generally govern hybrids. In such a process a mingling of the chromatin of two physiologic lines could occur, and from the resulting recombinations forms with parasitic capabilities different from either parent might arise.

Similar questions could be raised concerning the significance of the fusion of sporophytic germ-tubes and hyphae (p. 157). If the fusion of sporophytic hyphae between different physiologic forms should actually occur, as could easily happen, there would arise the problem of the resulting history of the nuclei and the effect on the pathogenicity of the rust.

Recently claim has been made that crossing two physiologic forms might be effected by suitably mixing the pycnial nectar with its pycniospores of one strain with that of another (Craigie, 1927b).

Such questions as these, as well as the possibility of mutations among the rusts, the latter a resort of many writers to account for variations, are yet almost wholly beyond any substantial basis of facts and consequently are matters of speculation.

Color mutation. — A change in the color of the urediniospores was observed in a single sorus in the seventh generation of *Puccinia graminis tritici* (Newton & Johnson, 1927b). This strain of rust had been grown in the greenhouse for four months, and through six generations had shown no deviation from the usual appearance. The mutating sorus gave orange-colored spores with colorless walls. A pure strain was obtained, which continued to produce only orange-colored spores for eight months. It did not differ from the parent strain in nuclear behavior or pathogenicity, but showed somewhat smaller spores and less vigor in germination.

The same observers also record a variation in color of urediniospores in the first generation from aecial infection, which persisted in subsequent generations. The change consisted in a deeper color in the cell-wall and loss of color in the cell contents, a change which is normal and usual in the production of resting spores, but in this instance the significance is not apparent.

Host stability. — The question of stability in the reaction of hosts toward their rust parasites may be attacked both from the physiologic side and the genetic side. The amount of sporulation is usually a fair index of the degree of development of the rust. The prime factor in the growth of the rust is the food supply, and this is dependent upon the vigor of the host (p. 239).

In some cases etiolated plants, or albinos after reserve nutriment of the seed has been exhausted, have been infected with no macroscopic evidence of the development of the rust; but when carbohydrates are supplied to the plants (Fig. 136) the rust is able to make as vigorous growth as in normal green plants (Mains, 1917, 1926b). It has been found that fertilizers change the relative amount of collenchyma and sclerenchyma in certain varieties of wheat and thereby modify the extent to which the rust thrives (Hursh, 1924). Changes induced by other parasites may influence the degree of sporulation, and possibly of susceptibility, as occurs with *Puccinia glumarum* when the host is *Triticum vulgare* infested with *Tilletia tritici* (Dillon Weston, 1927).

Fig. 136. — Leaf from a seedling albino plant of *Zea mays* (corn) infected with *Puccinia sorghi*. The rust obtains its nutriment from the supply still derived from the seed. (After Mains, 1926b.)

In general, conditions which modify the metabolism of the host have a more or less corresponding effect upon the development of the rust. It is probable that the effect of fertilizers, temperature, etc., in reducing or increasing the amount of rust in most instances may be explained by a change in the supply of available food for the parasite.

It does not appear, however, that resistance to infection is materially modified by any treatment accorded the host. In tests with *P. graminis* no variation in resistance has been detected when fertilizers were used with several varieties of wheat. In tests with *P. rubigo-vera tritici* some differences were found in the moderately susceptible wheat, Haynes Bluestem, but none with the highly resistant durum variety, Iumillo (Stakman & Aamodt, 1924). Varieties of wheat tested with *P. graminis* show no changes in reaction under different conditions of temperature (Peltier, 1923), and only slight changes in highly resistant forms when subjected to anesthetics (Stakman, 1914a).

The changes noted in susceptible plants doubtless are not due to modification of the factors determining susceptibility, but rather are associated with conditions which determine obligate parasitism. This

conclusion is supported by observations. It has been noted in a number of instances that there is a tendency for some varieties to show a much greater susceptibility in the seedling stage than when approaching maturity (Stakman & Piemeisel, 1917). Certain plants rated as heterozygous for susceptibility to *P. rubigo-vera tritici* are more or less resistant in the shooting and heading stages, but susceptible in the seedling stage (Mains, Leighty & Johnston, 1926).

CHAPTER VIII

TERATOLOGY AND PATHOLOGY

Abnormalities and diseases of the rusts: internal sori, malformed spores; abnormal germination, secondary bodies; nuclear disturbance; fungous parasites.

Pathologic changes in the host: dwarfing, chlorosis, leaf casting, necrosis, flecking, "green islands"; hypertrophy, galls, systemic infection, witches' brooms; geotropic response, rejuvenescence; anatomic changes; physiologic disturbances, transpiration, respiration, photosynthesis, chlorophyll, starch, calcium oxalate, resin, anthocyanin.

Pathologic injury to animals and man.

ABNORMALITIES AND DISEASES OF THE RUSTS

The rusts are subject to deviations from the usual or normal course of development while establishing their adjustment to the environment, and in this regard are not unlike other living organisms. As most of the vegetative body of the rusts is buried within the tissues of the host, and is therefore protected from the more pronounced environmental changes to which free organisms are exposed, not much aberration is to be expected in their vegetative parts, and in fact little has been observed. The noticeable abnormal changes in form or position, which might be classed under teratology, or in physiologic disturbance, which might be called disease, are almost wholly confined to the germ-tube, a normally free aerial organ, and to the reproductive parts, the sori and spores.

Internal sori. — Sori, whether formed within the tissues of the host, as in the majority of rusts, or in some instances partly or wholly exposed on the surface of the host, *e.g.*, in Olivea, Goplana, Hemileia, Cystopsora, Desmella and Calidion, ordinarily are so placed that the spores are discharged into the outside air. To open internally must defeat the purpose of their existence, and consequently sori so placed are to be considered abnormal and to be classed as "teratologic phenomena of no special morphologic significance" (Colley, 1918).

Pycnia belonging to *Uromyces pisi* have been found (Stämpfli, 1910) opening into the locules of Tithymalus (Fig. 137). Aecia opening toward the central axis of the host have been recorded for *Puccinia cari-bistortae* in stems of *Carum carvi* (Klebahn, 1899), for *P. angustata* in stems and petioles of Lycopus (Wolf, 1913), for *Cronartium ribicola*

in pine branches (Colley, 1918), and for *Gymnosporangium juniperi-virginianae* in fruit of the apple (Reed & Crabill, 1915). In the stems of Carum and Lycopus the aecial sori were opening into the central cylinder of disintegrating pith, in the pine they were directed into resin canals, and in the apple toward the core of the fruit.

Uredinia of *Puccinia graminis* on rye have been found discharging spores into the interior of the hollow stems (Wolf, 1913), and both uredinia and telia of *Cronartium ribicola* on Ribes have been seen with inverted position in stems and petioles (Colley, 1917a, 1918).

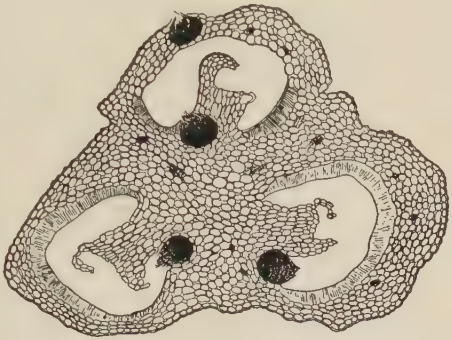


Fig. 137. — Four pycnia of *Uromyces pisi* in the fruit of Tithymalus, three of them opening into the locules. (After Stämpfli, 1910.)

In these examples of abnormal positions of sori there is a reversed polarity which directs the apex of the sorus toward some internal cavity or loose and defunct tissue. In normally placed sori only one important condition appears to dominate their orientation, and that is to bring the apex of the sorus through which the spores are liberated as near as possible to the free surface of the host and thus permit the spores upon dehiscence to be discharged into the external atmosphere. The nearest direction toward the surrounding air must be indicated by the penetration of gases through stomata or other openings in the epidermis. When sori arise deep in the tissues and the direction of aeration comes strongest from some cavity within the organ, the orientation of the sorus is affected accordingly and its usual position may be reversed. The reversed position of sori has also been ascribed to growth in the direction of least resistance (Wolf, 1913; Colley, 1918), but as the orientation of the sorus must be determined while in the primordial state, the determining factor would seem to be physiologic rather than mechanical.

Sori of various kinds often occur in unusual locations but directed outward, as, *e.g.*, deep-seated pycnia discharging their spores into intercellular spaces or into mature aecia (Fromme, 1914), a second pycnial layer arising below the normal one of *Cronartium ribicola* on pine branches (Colley, 1918), aecia of *Puccinia graminis* on cotyledons within the unopened seeds of *Berberis vulgaris* (Smith, 1886), uredinia and telia

within the caryopsis of cereals (Smith, 1886; Eriksson & Henning, 1896; Bolley & Pritchard, 1905; Pritchard, 1911), and uredinia of *Uromyces caryophyllinus* in the center of leaves of Dianthus (Adams, 1916). In these instances the polarity of the sorus is only occasionally affected, and the vigor of the rust in the particular organ is to be considered chiefly accountable for the location of the sorus.

Malformed spores. — Spores which conspicuously vary from the forms commonly associated with any particular species have attracted the attention of workers with the microscope for the past three-fourths of a century. They have usually been considered as curious deviations from normal development, occasionally they have been taken as the basis of new genera or species (p. 290) and more rarely they have been used to illustrate stages in phylogenetic progression.

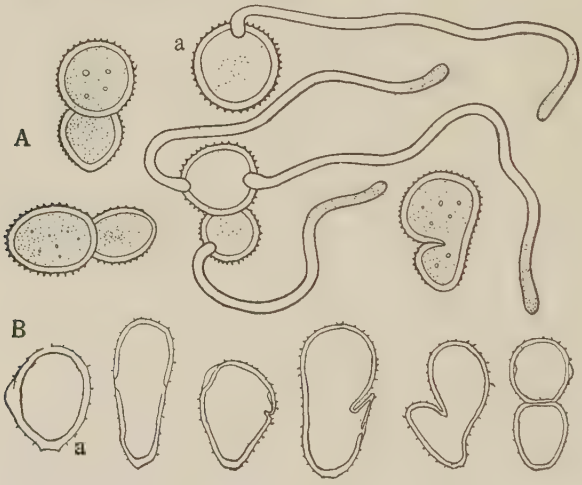


Fig. 138. — Urediniospores of *Puccinia chrysanthemi*, partly germinating: *a,a* normal form, the others variously abnormal. (*A* after Roze, 1900; *B* after Fischer, 1904.)

There is no record of aeciospores with more than one cell, and the only such record regarding urediniospores (Fig. 138) refers to their rare occurrence in *Puccinia chrysanthemi* (Roze, 1900; Jacky, 1900, 1903; Fischer, 1904). No apparent reason stands in the way of the division of the single cell in either aceiospores or urediniospores, and examples of such will doubtless be found eventually.

Among the aecia-like spores of the microcyclic *Endophyllum tuberculatum* on Malvaceae there often occur two-celled spores (Fig. 139), which vary externally only in being somewhat oblong and larger.

This rust was for a long time considered to be an Aecidium (*A. tuberculatum*), but is now known to be a short-cycle form correlated with the long-cycle form *Puccinia interveniens.*

The various kinds of malformations of teliospores may be conveniently grouped under four heads, *viz.*, (1) distorted shapes, (2) the abortion of one or more cells in a compound spore, (3) multiplication of cells by extra cross-walls, and (4) unusual position of the partitions. In all deviations gradations between the normal and abnormal forms can usually be found, and in some instances it is difficult to say where the line should be drawn between normal variation and teratologic freaks.

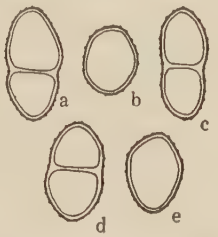


Fig. 139. — Microteliospores of *Endophyllum tuberculatum: a* taken from *Callirhoë involucrata, b, c* from *Althaea rosea, d, e* from *Sidalcea candida; b* and *e* show the normal form. (Original.)

Little need be said about distorted forms (Fig. 140). They are usually explainable by uneven compression or some accident of position or development. The outer spores of a sorus are more frequently affected both in size and form (Fig. 27). This difference between the peripheral and central spores of the sorus is usually ascribed to "a lack of nutriment and excessive pressure" (Bolley, 1889b), which dwarfs the spores and interferes with the formation of a cross-septum. However, if pressure enters into the problem, it must come from within the sorus rather than from without, as the same phenomenon is observable in the spore-heads of Ravenelia (Fig. 43 *B*), which are free bodies without external contact. As the outer spores of a sorus are usually formed later than the central spores it may be that they fail to receive the same amount of nutriment.

The abortion of one or more cells in a compound spore is a common occurrence, and becomes particularly conspicuous when the spore contains numerous cells, as in Phragmidium and Xenodochus (Fig. 141). No cytologic study has been made of such abnormal spores, and no suggestion in explanation of the cause is thus far forthcoming.

The multiplication of cells by extra cross-walls is also of common occurrence. The additional walls may be placed parallel to the normal walls or obliquely (Fig. 142). Although the development of such spores has never been studied, yet it is easy to see that many of the changes are due to an extra division of one or more of the normal cells of the spore. If the energy expended in producing a two-celled teliospore of Puccinia continues to act and one of the cells again divides,

a three-celled spore will result (Fig. 142 *c*), and if both cells divide, a four-celled spore results (Fig. 142 *d*). Such a process may be continued, and spores arise with a still greater number of cells. The occur-

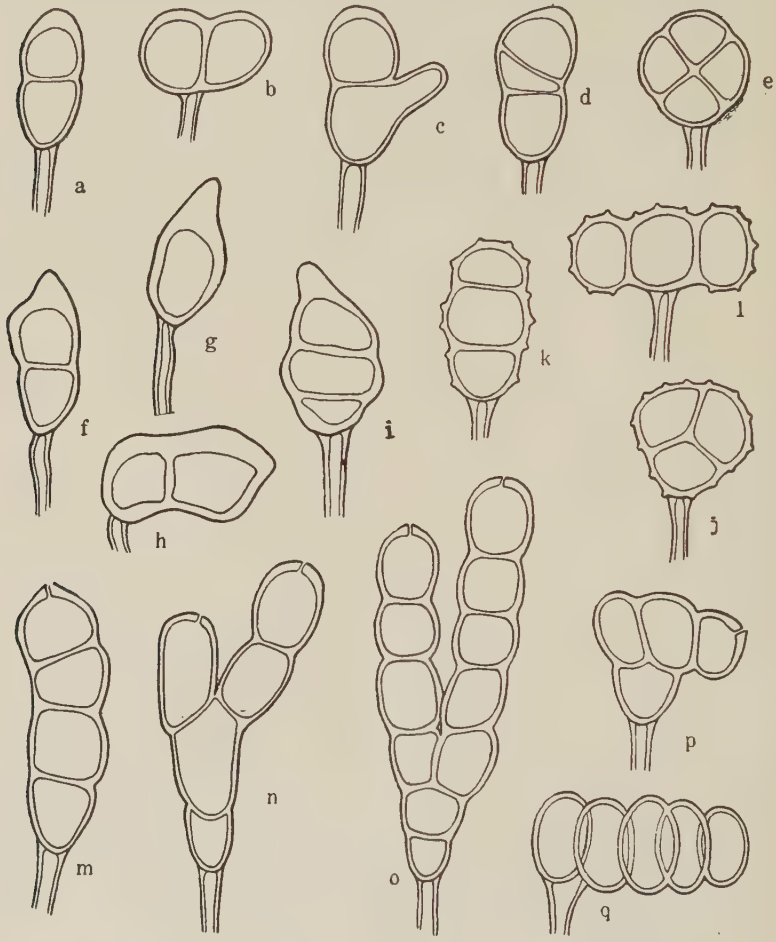


Fig. 140. — Malformed teliospores: *a–e Puccinia windsoriae* on Tridens, *f–i P. irregularis* on Verbesina, *j–l Triphragmium ulmariae* on Filipendula, *m–q Frommea obtusa* on Potentilla; *a*, *f*, *j*, *m* normal forms, the others distorted. (*a–e* after Warren, 1898; *f–i* after Hume, 1899; *k–l*, *n–q* after Dietel, 1887; *j*, *m* original.)

rence of supernumerary cells is not uncommon in spores of the Pucciniaceae, but is rare in spores of the Melampsoraceae (Fig. 143).

Some genera of rusts possess teliospores with definitely normal oblique

FIG. 141. — Teliospore of *Phragmidium fusiforme* on Rosa: upper cells abortive. (After Fischer, 1904.)

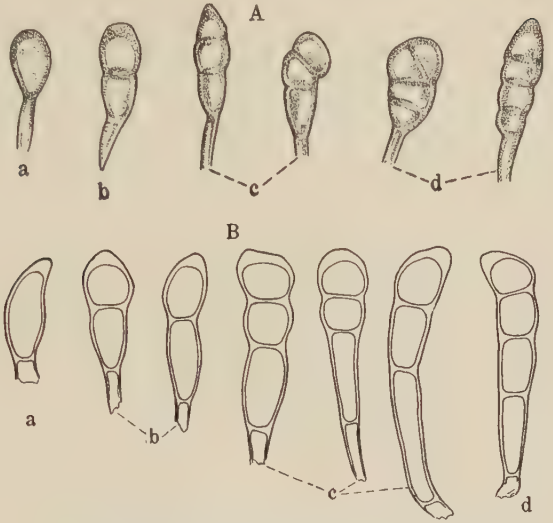
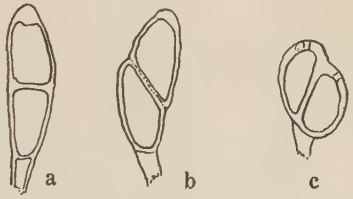


FIG. 142. — Variation in number of cells in teliospores of *Puccinia graminis A*, and *P. scleriae B: a* one-celled (mesospore), *b* two-celled or normal form, *c* three-celled by division of the upper cell, *d* four-celled by division of both upper and lower cells. Two of the spores with oblique walls. (*A* after Hume, 1899; *B* original.)



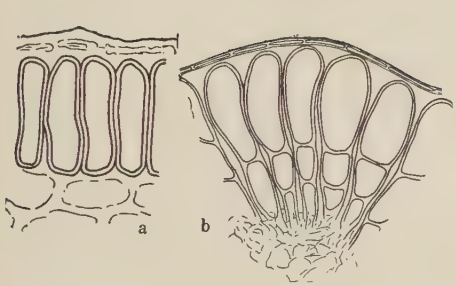


FIG. 143. — Teliospores of *Melampsora medusae* on Salix: *a* normal one-celled spores, *b* two- and three-celled spores. (Original.)

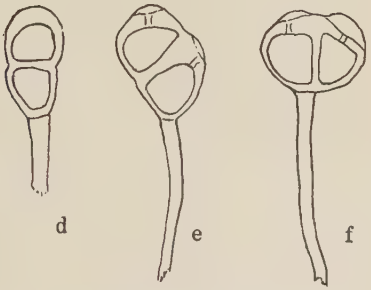


FIG. 144. — Teliospores of grass rusts that commonly have the septum oblique: *a–c Puccinia flaccida, d–f P. levis.* Magnified about 400 diameters. (Original.)

walls, *e.g.*, Triphragmium (Fig. 25 *k*), Sphaerophragmium, Nyssopsora (Fig. 25 *p*), but when the cross-wall of a teliospore belonging to a genus with normally transverse walls is laid down obliquely, the angle may vary from a slight deviation from the normal position to a position approximately vertical (Fig. 144). This change in direction of the septum frequently appears to be associated with a change in the attachment of the pedicel, and the pedicel is described as placed obliquely. This, however, is rarely if ever the true condition. The polarity of the spore, as indicated by the hilum and the apical thickening opposite to it is rarely disturbed, whatever the deflection of the septum, even in extreme instances. In contrast to such occasional changes the genera Diorchidium (Fig. 25 *q*) and Sphenospora have the teliospore divided normally into two cells by a truly vertical septum as shown by the equal attachment of both cells to the pedicel and the equal thickening at the apices of the cells (Fig. 25 *q*), which is unlike the teliospores of *Puccinia vertisepta* (Fig. 145), a rust on Salvia in Mexico, which was once erroneously referred to Diorchidium. Oblique septa are so abundant in some species with normally transverse septa as to be characteristic and attract special attention, *e.g.*, *Puccinia flaccida* (*P. abnormis*, *P. subdiorchidioides*) on Panicum (Fig. 144 *a–c*), *P. levis* on Panicum and Paspalum (Fig. 144 *d–f*), *P. dochmia* on Muhlenbergia and *P. exasperans* on Bouteloua, all grass rusts from subtropical regions. Gradations from the typical puccinial form of teliospore to extreme obliquity are usually present in each instance.

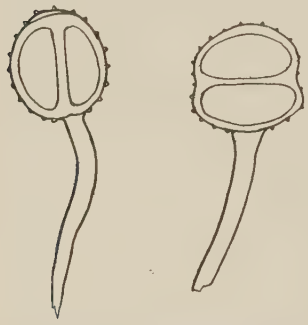


FIG. 145. — Teliospores of *Puccinia vertisepta*, showing extremes in position of the septum. (Original.)

Variation in the structure of the spore from the norm of the species, due to number and position of the septa, is clearly to be considered a teratologic feature, a monstrosity or abnormal development. Furthermore, such unusual forms show a tendency to become hereditary, a well known teratologic characteristic among flowering plants. There are two notable examples of this feature among the grass forms of *Puccinia rubigo-vera*, both occurring in northern regions. The genus Rostrupia was founded by Lagerheim (1889) upon forms on Elymus having more than two lineally arranged cells in the teliospore (Fig. 146).

Puccinia tomipara was founded by Trelease (1885) on forms on Bromus, having a variable number of teliosporic cells, often separated by oblique or vertical walls in a muriform manner (Fig. 147), and was afterward referred to the genus Rostrupia by Lagerheim (1889). In both of these instances the aecia occur on Thalictrum, but the variation from the normal in the form of the teliospores apparently has reached hereditary permanency, producing fairly well established races. *Puccinia rubigo-vera tomipara* has been cultured by Fraser (1920).

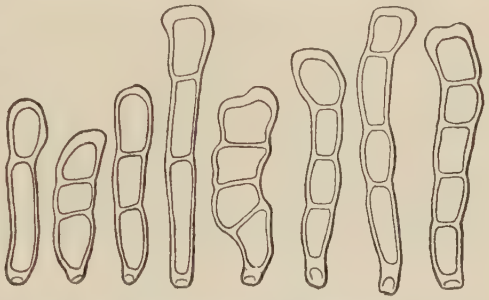


Fig. 146. — Teliospores of *Rostrupia elymi*, a teratologic race of *Puccinia rubigo-vera* on Elymus. (After Lagerheim, 1889.)

The line of separation between the expected oscillating variation of a species having a two-celled teliospore and the extreme saltation which marks a racial or teratologic departure is difficult to define. If the two-celled teliospore is to be taken as the normal feature of the genus Puccinia, and forms with more than two cells in the teliospore are to be considered aberrations, and when well established viewed as races, then forms with less than two cells in the teliospore may logically be treated in the same way.

Fig. 147. — Teliospores of *Puccinia rubigo-vera* on Bromus from the race called *P. tomipara*, mostly with abnormally divided spores. (Original.)

The genus Puccinia was for a time composed of two sections, one having two-celled and the other one-celled spores. The forms with one-celled spores were given the name of Uromyces in 1816, and erected into a genus in 1833, but the wisdom of this was called in question by Tulasne (1854b), who said: "The Uromyces are Puccinias reduced to a single cell, the Pucciniolas as L. Marchand calls them. . . . In *Puccinia sonchi* Rob. the uromycetous spores are not at all rare, for they are often more abundant than the bicellular spores; and as this species is probably not the only case, the autonomy of Uromyces

is a grave question." The opinion of Tulasne has been upheld and strengthened by many writers since, and the relation of Uromyces to Puccinia shown to be even more intimate (Orton, 1912), until all species of Uromyces are now quite generally regarded as properly belonging under the genus Puccinia, and kept apart only as a matter of convenience.

The number of cells in the teliospore plays so small a part in distinguishing well founded genera among Uredinales that the arguments brought forward from teratologic evidence (Dietel, 1887; Lagerheim, 1891; Vuillemin, 1893a; Warren, 1898; Hume, 1899) have small weight in tracing phylogeny.

While in the preceding instances teratologic forms of spores have been induced presumably by accidental or hereditary influences there is one record in which nutrition of the host appears to have had some effect. *Puccinia rubigo-vera tritici* on *Triticum vulgare* was grown in Petri-dishes with sugar solution by Waters (1928) and found to produce "many abnormal spores, some thick-walled, one-celled with spines, others two-celled with spines, and some like the typical two-celled, smooth-walled teliospores."

Abnormal germination. — Although variations in light, heat, moisture, various solutes and gases, especially oxygen, may and usually do produce an effect upon the normal growth and behavior of the rusts in all their stages, yet few instances of marked pathologic or teratologic results have been observed, except in the parts that develop outside the host. The growth of the germ-tubes from teliospores, aeciospores, urediniospores, basidiospores and pycniospores, when proceeding under unfavorable conditions, give morphologic evidence of disturbed metabolism.

The development of the germ-tube or promycelium from the teliospore normally takes place in the air as a free upright organ of definite length and form, if the temperature is not too high (p. 226). When the germ-tube is submerged, however, as usually occurs if the germination of teliospores is tested in a hanging drop, or the air is exhausted, all degrees of abnormality are likely to result. The germ-tube may grow very long (Fig. 148) and continue without septation until the stored energy of the cell is exhausted, although it may branch. When septation takes place the cells may round off and separate (Fig. 149), like an oïdium (Carleton, 1893). The oïdium-like cells may form sterigmata bearing spore-like bodies (Fig. 149 *d*), or they may produce long hypha-like growths (p. 226). That such cells are capable of starting an infec-

tion in a suitable host is highly improbable. No cytologic or cultural studies have been made.

Aeciospores and urediniospores normally develop best in a film of water or a saturated atmosphere, and the germ-tube resembles a hypha

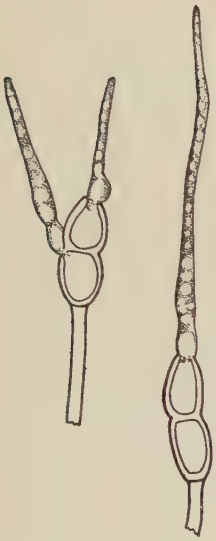


Fig. 148. — Germination of *Puccinia arenariae* submerged in water, with indefinite and unseptated promycelium. The protoplasm is filled with large vacuoles. (After Lindfors, 1924.)

Fig. 149. — Abnormal germination of *Puccinia malvacearum: a–e* submerged in a hanging drop; *f*, *g* in rarified air under the bell-jar of an air pump; *h* in water between glass slide and cover-glass with air exhausted. (After Klebahn, 1914, except *e* which is after Sappin-Trouffy, 1896.)

of moderate length without branches or septation. When submerged, however, the growth continues until the food supply within the spore is consumed, and more or less branching, septation and distortion occur.

The pycniospores show growth only in a sugar solution. What relation, if any, this physiologic fact holds to the secretion of a sugary solution usually accompanying the aecia is not known, as no morphologic action of the pycniospores has been positively demonstrated. The small germ-tube which they sometimes emit (Carleton, 1893; Sappin-Trouffy, 1896) has a very limited growth, and may be an incid-

ental production, as it can plausibly be surmised that in the original functional state the pycniospore required contact with another body. The formation of secondary pycnial bodies has also been seen (Cornu, 1876b; Plowright, 1889; Carleton, 1893; Sappin-Trouffy, 1896).

The basidiospores in germination behave much like the pycniospores, except that growth takes place in water or a saturated atmosphere, and is not hastened by a sugar solution. When the basidiospore in normal development comes in contact with the epidermis of a plant, it pierces the cuticle and the outer wall of the epidermal cell by a very fine extension, which again swells to full size within the cell. This behavior was accurately observed by de Bary (1853), who also noted that when such contact was not possible the basidiospores "did not delay to put forth a germ-tube, short and slender, which was able to produce secondary sporidia, but it is with this production that the growth reaches its limit." The formation of slender germ-tubes or secondary spores in the germination of the basidiospore has been noted in many genera by numerous observers, as in *Chrysomyxa abietis* (Reess, 1869), in *Gymnosporangium clavariaeforme* (Plowright, 1889), in *G. cunninghamianum* and *Uromyces cunninghamianus* (Barclay, 1890), in *Gallowaya pinicola* (Galloway, 1896), in *Puccinia coronata avenae* (Eriksson & Henning, 1896), in *P. malvacearum* (Taubenhaus, 1911), in *Gymnosporangium juniperi-virginianae* (Reed & Crabill, 1915), and in *Cronartium ribicola* (Colley, 1918; Clinton & McCormick, 1919; Spaulding & Gravatt, 1925, 1926).

Secondary bodies. — When the conditions are not present for the continuation of normal growth during germination a secondary and somewhat similar form may result, only smaller and less perfect. Among higher plants it is a familiar phenomenon; with potato tubers especially when moisture is partially excluded, small tubers form on the surface of the parent, or even within it.

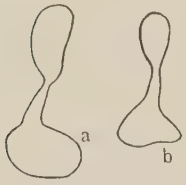


Fig. 150. — Two basidiospores forming secondary bodies: *a Coleosporium tussilaginis*, *b Puccinia moliniae*. (After Tulasne, 1854b.)

The "secondary sporidia," observed by de Bary (1853), Tulasne (1854b) and many others, arising from basidiospores were of this nature (Fig. 150), and also the secondary bodies arising from pycniospores (Cornu, 1876b; Plowright, 1889; Carleton, 1893; Sappin-Trouffy, 1896). However, the yeast-like growth seen by Plowright, taking place in honey and water and drawn after twelve hours and again after six days, suggests the probability of yeast contamination.

Such translocation of the contents of spores into secondary bodies has been figured by Sappin-Trouffy (1896) for aeciospores of *Uromyces erythronii* (Fig. 151), *Puccinia rubigo-vera secalis*, *Gymnosporangium clavariaeforme*, *Coleosporium senecionis*, and for urediniospores of *Puccinia graminis* (Fig. 152), *P. polygoni-amphibii* and *Phragmidium rubi*. Figures for urediniospores producing secondary bodies have also been

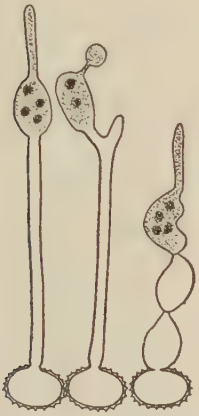


Fig. 151. — Abnormal germination of aeciospores of *Uromyces erythronii*, showing translocation of the contents of the spores into secondary bodies. (After Sappin-Trouffy, 1896.)

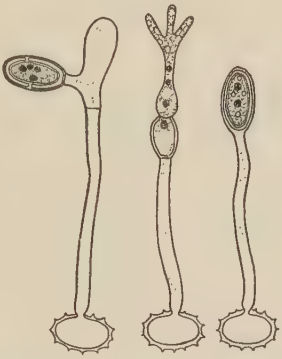


Fig. 152. — Abnormal germination of urediniospores of *Puccinia graminis*, showing translocation of the contents of the spores into secondary and tertiary bodies. (After Sappin-Trouffy, 1896.)

published for *Cronartium flaccidum* (Tulasne, 1854b), *Puccinia graminis* (Plowright, 1889), *P. iridis* and *P. fagopyri* (Barclay, 1890). It has been found that an increase in abnormal germination of urediniospores of *Cronartium ribicola* occurs when the spores are grown in weak solutions of organic acids, especially lactose with addition of gallic acid (York, see Spaulding, 1922).

The secondary bodies which are formed in germination vary from simple vesicles to variously distorted bodies, or well-shaped bodies resembling the original spore. The walls may be thin and colorless, or thickened and sculptured like the original spore. Usually the growth impulse does not cease with the formation of one secondary body, but may produce a tertiary body, or may push out simple or branched tubes. The distorted forms that may arise are unlimited so long as growth continues.

It has not been shown, and seems wholly improbable, that infection can result from the debilitated so-called secondary or tertiary basidiospores. The inference is at present unsubstantiated that the formation of such a body "is probably to tide it over unfavorable conditions of infection" (Clinton & McCormick, 1919), or that in *Cronartium ribicola* such bodies "are potentially dangerous to pines for much longer periods than the longevity of the primary sporidia would indicate" (Spaulding & Gravatt, 1926).

Nuclear disturbances. — The number of nuclei in a cell of the rusts is not uniform, but the norm, or standard number, is assumed in any discussion to be one for each cell in the gametophytic phase and two for each cell in the sporophytic phase (p. 116). This is the usual condition for most macrocyclic species possessing all the spore forms, *e.g.*, *Puccinia graminis*, *P. violae*, *Uromyces caladii*, *U. erythronii*, *Coleosporium sonchi*, *Melampsora lini*, but occasionally some of the cells preceding formation of the hymenium are binucleate, *e.g.*, in *Puccinia caricis* (Kursanov, 1910), and rarely a uninucleate condition of hymenium and aeciospores has been detected, *e.g.*, *Tranzschelia punctata* and *Ochropsora sorbi*, both found on Anemone in central Russia (Kursanov, 1910).

When uredinia are omitted from the cycle, as in species of Gymnosporangium and Gymnoconia, the normal course is less uniformly followed. The binucleate condition often anticipates the change from gametophyte to sporophyte.

In microcyclic species deviations from the norm are much oftener met with, and in greater variety. The precocious appearance of the binucleate condition in the gametophyte is common, and a continuation of the uninucleate condition throughout the whole cycle is known in several instances, *e.g.*, *Endophyllum euphorbiae*, *Kunkelia nitens*, *Uromyces rudbeckiae* (p. 159).

Beside the more or less regular increase or decrease in the number of nuclei, there occur occasional changes having doubtful significance. Binucleated basidiospores have been seen in species belonging to several genera (p. 157), and multinucleated aeciospores are not rare (Fig. 113). Aeciospores with three to seven nuclei (p. 156) have been recorded for *Phragmidium violaceum* (Blackman, 1904), *Melampsora lini* (Fromme, 1912), *Endophyllum sempervivi* (Hoffmann, 1911), *Uromyces caladii* and *Puccinia claytoniata* (Fromme, 1914), while urediniospores with five nuclei have been seen in *Puccinia suaveolens*, and microteliospores with three to six nuclei in *Chrysomyxa abietis* (Kursanov, 1910). Cells with

a few nuclei have been found to arise by cell fusion, but "it is inconceivable that a 7-nucleated aecidiospore which was found in an aecidium, the other spores of which were mostly uninucleated, could have been the result of the fusion of seven cells" (Dodge, 1924c).

The most outstanding suggestion to be drawn from these aberrancies in nuclear behavior, spore germination, etc., is their apparently high correlation with reduction in the life-cycle. When a rust starts to shorten its cycle from a full macrocyclic to a microcyclic condition it may begin to wobble like a mechanism without a steering apparatus, and almost any sort of vagary may result. Very few, if any, of these changes from the norm can be considered pathologic, but are more properly classed as teratologic.

Enlarged and deformed nuclei are not infrequently met with (p. 232), however, which indicate a truly pathologic disturbance, as in *Puccinia violae* (Reynolds, 1912) and in *P. graminis* (Allen, 1923b).

Fungous parasites. — Many species of fungi have been found associated with the sori of rusts, but it is difficult to decide whether the connection is that of parasitism or merely of convenience. Some of the species are undoubtedly parasites, as for example, *Darluca filum*. No comprehensive study of the subject has yet been made. The following enumeration includes most of the records at the present time. The synonymy is in need of critical revision, but the descriptions can be found in large part in Saccardo's Sylloge Fungorum.

Chytridiales: Olpidiella uredinis Lagerh., within the urediniospores of *Uredo airae, Puccinia violae, P. coronata,* and *P. levis.*

Ascomycetales: Melanomma loepophagum (Tul.) Sacc., on *Peridermium acicolum; Sphaerella pucciniophila* Sacc. & Syd., on *Puccinia malvacearum.*

Phyllostictales: Ascochyta contubernalis Oud., on *Uromyces acetosae,* which may be a Darluca, according to Hariot; *Darluca arcuata* Ellis & Ev., on uredinia on Andropogon; *D. bubakiana* Kabát, on uredinia of *Frommea obtusa; D. filum* (Biv.) Cast., on aecia, uredinia and telia of many rusts; *D. genistalis* (Fries) Sacc., on *Uromyces genistae-tinctoriae; D. gen. hypocreoides* Fuckel, on uredinia on Salix; *D. gen. stromatica* Fuckel, on uredinia on *Agrostis stolonifera; D. mucronulata* Oud., on Puccinia on grass and sedge; *D. sorghi* Zimm., on *Puccinia purpurea; Discosia podisomatis* C. & E., on *Gymnosporangium juniperi-virginianae; Phyllosticta pucciniophila* Massal., on *Puccinia malvacearum; Septoria parasitica* Fautrey, on *P. malvacearum.*

Hyphomycetales: Botrytis uredinicola Peck, on *Uromyces graminicola; Cladosporium aecidiicola* Thüm., on Puccinia and Coleosporium; *Fusarium aecidii-tussilaginis* Allesch., on *Aecidium tussilaginis; Fusarium parasiticum* Ellis & Kellerm., on *Puccinia seymeriae* and *P. menthae; F. spermagoniopsis* J. Müll., on *Phragmidium subcorticium* and *P. rubi; F. uredinicola* J. Müll., on uredinia on Rosa and Rubus; *Fusoma rubrum* Lindau, on aecia on *Platanthera bifolia; Macrosporium podophylli* Ellis & Ev., on aecia of *Puccinia podophylli; M. uredinis* Ellis & Barth., on *P. graminis; Monosporium uredinicola* Stevens, on *Coleosporium ipomoeae; Ramularia coleosporii* Sacc., on Coleosporium; *R. uredinis* (Voss) Sacc., on *Melampsora bigelowii; Tuberculina aecidiophila* (Speg.) Pat., on *Puccinia hyptidis; T. barteti* Vuill., on *Peridermium barteti; T. flavogranulata* Dearn. & Barth., on *Uromyces hedysaripaniculati; T. maxima* Rostr., on aecia of *Cronartium ribicola; T. malvacearum* Speg., on *Puccinia heterospora; T. ovalispora* Pat., associated with *Darluca filum; T. persicina* (Ditm.) Sacc., on many species of rusts; *T. phacidioides* (Dur. & M.) Sacc., on aecia of *Puccinia magnusiana; T. pirottae* (Speg.) Sacc. on *P. malvacearum; T. ricini* (Cocc.) Sacc. & Syd., on uredinia of *Melampsorella ricini; T. sbrozzii* Cav. & Sacc., on *Puccinia vincae; T. vinosa* Sacc., on various aecia.

PATHOLOGIC CHANGES IN THE HOST

When mutual tolerance is established between the parasite and its host little or no disturbance in the normal course of development of either organism is noticeable, unless the supply of nutriment proves deficient. When, however, the host reacts upon the parasite to check its growth, a more or less pronounced immunity is established. Or when the parasite reacts upon the host by irritation, repression or stimulation, a greater or less disturbance in form or function of the latter results.

The strongly obligate parasitism of the rusts is attested by the comparatively slight injury inflicted upon the hosts, and then usually only in one of the antithetic stages, except in so far as any diversion of the food supply may prove inimical to full development. Almost the whole economic loss from rusts in cultivated plants is traceable to the inability of the host to meet the excessive demands of the parasite for nutriment, rather than to injury by the death or absorption of a part or whole of the host, as occurs with some other fungous parasites, notably the smuts.

The symptoms of disease produced by rusts upon their hosts, although varied, may be grouped under the general terms *hypoplasia*, dwarfed or retarded growth, *necrosis*, a disorganization leading to death, and *hypertrophy*, the enlargement of tissues and organs. These three classes of symptoms are rarely, if ever, specifically manifested in their strict interpretation, but usually present a complex which varies not only with the conditions and tissues of the host but also with the phases of the rust. Underlying these visible external symptoms are physiologic disturbances resulting in more obscure histologic changes in the tissues and variations in the cell contents. The principal forms of pathologic reaction of the host induced by rusts are reviewed in the following paragraphs. Many features of the subject, however, have received but slight or no attention from investigators.

Dwarfing (*hypoplasia*). — Hypoplastic effects are often brought about indirectly or directly by the action of the parasite. The fungus may divert a large part of the nutriment provided by the host or inhibit its usual production and thus partially starve the tissues. The result is smaller leaves and fruit and shorter stems. But the direct effect of hypoplastic influence is seen when tissues within the area invaded or directly influenced by the mycelium fail to attain their normal size. As the supply of nutriment for the rust is entirely derived from the host, the latter must necessarily suffer proportionally. A common result of this diversion of nourishment to the rust is to check the development of the host, and usually to a degree that roughly corresponds to the extent of the invasion of the host by the parasite.

As a rule the rusts are so well adjusted parasitically to the hosts in which they grow that small change is observable in the appearance and size of the supporting plants. In the stem rust of wheat, *Puccinia graminis tritici*, even under heavy infection, the height of the plant is not much reduced, although more or less reduction takes place in all its parts, especially in the flowers and seeds. With the leaf rust, *P. rubigo-vera tritici*, the result is usually the same, but not so marked (pp. 327, 333). Similar changes can be seen in other grass and sedge rusts.

With *P. antirrhini*, the rust of snapdragon, when heavy infection occurs while the plant is still young, not only the plant as a whole is much smaller, but the leaves are shorter and thicker and the inflorescence is partly or wholly abortive. In the case of the uredinia of *Melampsoropsis pyrolae*, in which infection takes place in the fall of the year

on the very young leaves of Pyrola that are to develop in the following spring, little or no change during their growth is apparent in size or color, although the mycelium may spread throughout the blade of the leaf, causing a systemic infection.

Fig. 153. — Systemic invasion in a perennial plant, *Hepatica acutiloba*, by the perennating gametophytic mycelium of *Tranzschelia punctata:* the normal leaves are prostrate, the infected leaves are smaller and upright. (Original.)

The examples mentioned are all taken from the sporophytic growth of the rust. The same results also come from the gametophytic growth, only they are often much more pronounced. The aecia of *Tranzschelia punctata* on Anemone and Hepatica (Fig. 153), of *Ochropsora sorbi* also on Anemone, and of *Cerotelium dicentrae* (*Aecidium dicentrae*) are comparable in their effects with the uredinia of *Melampsoropsis pyrolae*, but cause more change in the host. Still more pronounced dwarfing occurs with *Uromyces pisi*, *U. occidentalis*, *U. caryophyllinus*, and other species having their aecia on Tithymalus.

All the preceding examples are from heteroecious rusts, but the same results follow in the gametophytic stage of some autoecious rusts, *e.g.*, *Uromyces proëminens* on Chamaesyce (Fig. 154), as well as in many microcyclic rusts, as *U. scutellatus*, *U. tranzschelii*, *Puccinia holboellii*, and *P. physostegiae*.

Chlorosis. — The loss of chlorophyll pigment resulting in a yellow color, which occurs in the cells of certain definite areas although the chloroplasts may be otherwise normal, is given the term chlorosis. It is associated with the immediate presence of the mycelium of the

rust, either localized or systemic, but its direct cause has not been investigated. It is a symptom to be sharply separated from the general indefinite yellowing of the plant due to a lack of nutriment or a lowered vitality resulting from any cause, parasitic or non-parasitic.

FIG. 154. — Systemic invasion in an annual plant, *Chamaesyce serpyllifolia*, by *Uromyces proëminens:* the branches bearing aecia stand upright, with elongated internodes and no flowers, while the branches bearing uredinia and telia are prostrate, with normal leaves and inflorescence. (Photograph by H. L. Lyon.)

Chlorosis is particularly noticeable in the area immediately surrounding a group of sori from localized mycelium, especially those of aecia, sometimes but less marked, those of uredinia, and rarely if ever of telia. In *Aecidium hydnoideum* on *Dirca palustris* the chlorotic spots are usually sharply defined and circular, often reaching a diameter

of a centimeter or more, making an infected shrub conspicuous at considerable distances.

A marked instance of chlorosis is found in *Peridermium corruscans* (Fig. 155), which attacks the buds of *Picea alba* in northern Europe. The rust produces a hypertrophic chlorosis of the young shoot, but does not induce the growth of adventitious buds, as occurs in the formation of witches' brooms. The soft, early growth is edible (Tubeuf, 1897).

Fig. 155. — A branch of *Abies alba* bearing three hypertrophied shoots infected with *Peridermium corruscans* bearing aecia. (After Tubeuf, 1897.)

In witches' brooms produced by the systemic growth of gametophytic mycelium (p. 310), the entire portion of the plant affected, both stem and leaves, becomes of a uniform pale-yellow color. Witches' brooms of this nature, *e.g.*, those of *Melampsorella elatina* on Abies and *Uromyces proëminens* on Chamaesyce, are highly conspicuous objects. Similar witches' brooms produced by sporophytic mycelium, *e.g.*, those of *Gymnosporangium juvenescens* and *G. nidus-avis* on Juniperus, do not exhibit chlorosis (p. 313).

Leaf casting. — A common and highly injurious action of the rust toward its host is a full or partial defoliation, or leaf casting. Heavily infected leaves often show premature ripening, become yellowish, shrivel, and finally drop, the oldest leaves on a stem falling first.

Apple trees when subjected to a heavy basidiosporic infection from *Gymnosporangium juniperi-virginianae*, may not only lose a large part of their foliage but even the fruit may drop (Reed & Crabill, 1915; Giddings & Berg, 1915a; Giddings, 1918). When the defoliation continues for successive seasons such trees are sometimes so retarded in their growth that they do not reach the size of a normal tree of five years until after seventeen to twenty years have elapsed (Reed & Crabill, 1915). In Europe heavy basidiosporic infection on spruce (Picea) from *Melampsoropsis rhododendri* (*Chrysomyxa rhododendri*) sometimes almost wholly strips entire forests of their foliage, leaving only a few healthy needles here and there (Tubeuf, 1897). Almost equal injury is frequently caused by the microcyclic rust, *Chrysomyxa abietis* on the same species of spruce (Willkomm, 1866; Reess, 1869).

The same kind of injury to the scrub pine, *Pinus virginiana*, in eastern United States by *Gallowaya pinicola*, has been carefully studied (Galloway, 1896).

Similar results may follow heavy infection of certain herbaceous plants. It is stated (Fromme & Wingard, 1918) that in the southeastern United States bean rust, *Uromyces appendiculatus*, sometimes brings about leaf-fall and ultimate death of susceptible varieties, and may reduce the annual yield to practically nothing. Early dropping of leaves from stems of *Asclepias syriaca* caused by *Uromyces asclepiadis* has often been observed, all the leaves for the season being piled about the base of the plants, each leaf bearing a heavy coat of brown spores.

All degrees of dwarfing from slight to extreme effects, whether due to the direct action of the rust or to leaf casting, are of common occurrence. It constitutes one form of arrested development, and is traceable to a scanty residual nourishment of the host. Such restricted changes from normal development, whether due to rusts or other agencies are comprised under the general term of hypoplasia (Küster, 1915).

Necrosis. — The death of cells, organs, or of entire plants, that is, the condition known as necrosis, is comparatively rare in connection with rusts. The mutualistic relationship of the rust and its host is usually so well adjusted that to produce the death of the host or any part of it must be considered as a rather extraordinary effect, since it would be inimical to the perpetuation of the rust and contrary to its usual behavior within the host. At no time does the rust develop in the host as a saprophyte, as with many other fungi, and consequently can not strictly be said ever to induce a necrotic disease.

The most marked necrosis is produced when the infected region is sufficiently extensive to cut off in large part or wholly the supply of water and nutrients to the parts beyond. This effect was noted by Mains (1917) in leaves of *Puccinia sorghi*. The dwarfing and eventual death of terminal portions of branches, and of seedling trees, is a commonly observed phenomenon. It is one of the serious injuries caused by the invasion of *Cronartium ribicola* into young trees of the five-leaved pines (Spaulding, 1914, 1922; Clinton & McCormick, 1919). The same destructive results are produced on pines by *C. cerebrum*, *C. pyriforme*, and *C. harknessii*, the last two species occurring exclusively in North America. The same destructive result is brought about by *Melampsora pinitorqua* when it passes from various species of Populus to *Pinus sylvestris* and *P. montana* (Tubeuf, 1897), being able to kill young trees.

Because the aecia of this rust make the shoots twist about at the place of attack (Fig. 156), the rust is commonly called "pine-twister" (*Kiefern-dreher*). Large trees as well as small ones may occasionally be killed by a method of girdling, when the rust extends around the limb and interferes with the free movement of sap. Spaulding (1914) reports the case of a tree about twenty years of age, which had been infected by *Cronartium ribicola* in the trunk about ten feet from the ground, and the death of the entire top above the point of infection had followed.

FIG. 156. — *Melampsora pinitorqua* infecting the shoots of Pinus and causing "pine-twisters." (After Hariot, 1908.)

The highly destructive rusts here mentioned and others of like nature belong to the Melampsoraceae. The only species at all comparable in destructiveness among the Pucciniaceae are *Puccinia corticola* of Trinidad (Arthur, 1922b), which not only attacks the leaves and twigs, but causes large lesions in the trunk of the timber tree, *Cordia gerascanthus* (Fig. 157), and also a few species of Gymnosporangium, notably *G. effusum* and *G. betheli* on species of Juniperus and *G. botryapites* on Chamaecyparis in the United States.

The heavy drain on the resources of the host when unusually severe infection has occurred often causes exhaustion that not infrequently results in the partial or total death of an organ or of the whole plant. It is a phenomenon very familiar to culture workers.

When exhaustion of the host caused by defoliation is continued for successive seasons the whole plant may die. Heavy aeciosporic infection of Ribes by *Cronartium ribicola* was observed (Pennington, 1922) to bring about the loss of foliage and final death of the plants after three successive seasons.

Among herbaceous plants it is recorded that death occasionally follows marked exhaustion from snapdragon rust, *Puccinia antirrhini* (Peltier, 1919; Doran, 1921), and asparagus rust, *P. asparagi* (Smith, 1905).

The debilitating effects of chlorosis (p. 300), when continued over a considerable period of time, may result in necrosis of the affected parts.

Flecking. — When small areas of the surface of leaves from two to five millimeters across, turn yellow and die, especially when such spots are numerous, the appearance is termed "flecking." It is usually brought about by abortive uredinial infection, and is especially noticeable on the leaves of cereals (p. 233).

The entry of a germ-tube into an uncongenial, resistant, or immune host is generally followed by changes in the cells with which the fungus comes in contact. In accordance with the virulence of the attack a few or many cells are gradually weakened and finally die, giving a characteristic spotted appearance (Ward, 1901, 1902c, 1903a; Gibson, 1904; Marryat, 1907; Stakman, 1914a, 1915; Allen, 1923a, b).

Fig. 157. — Lesions produced by *Puccinia corticola* in the trunk of a five-year-old tree of *Cordia gerascanthus* in Trinidad. (After Arthur, 1922b, photograph by Rorer.)

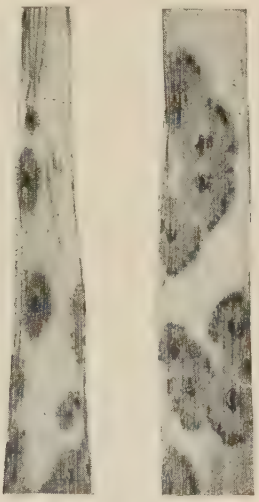


Fig. 158. — "Green islands" shown as a darker area between the primary and secondary uredinia. (Original, photograph by Mains.)

Under these conditions a few haustoria may be formed, but the parasite gradually dies from starvation or toxins, usually in four to fifteen days.

"Green islands." — The appearance not infrequently met with, in which a part of the infected area remains green after the surrounding

tissue has become necrotic is termed "green islands," and has been well described by Mains (1917) and Rice (1927) in the leaves of corn bearing *Puccinia sorghi.*

The cells near the primary uredinium, invaded by the haustoria, retain the characteristic color of healthy cells, and are bordered by a ring of secondary uredinia. The cells surrounding and extending beyond the infected area show a loss of starch, followed by yellowing and finally by death. The green area with its sori may continue to produce spores for some time (Fig. 158). The death of the "islands" finally results by their isolation from the healthy regions and the interruption in the flow of nutriment, or in part by the loss of water escaping into the surrounding dead area.

A somewhat similar condition has been described by Molliard (1895), where chlorophyll occurs in the tissues surrounding the sori on the colorless petals of *Euphorbia cyparissias* attacked by *Uromyces scutellatus.* In instances of this kind the green area supporting the sori is formed in tissues that normally produce no chlorophyll. Sometimes in chlorophyll-bearing tissues, especially under conditions unfavorable for continued host metabolism, a darker green is produced than occurs in the uninfected tissues. This result may be part of the stimulatory effect that the initial invasion of a rust often induces (Allen, 1926a).

Hypertrophy. — A more or less marked hypertrophy or swelling of the host occurs in many instances. It was one of the earliest specific

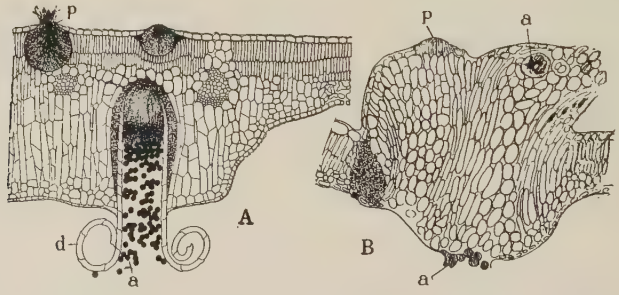


Fig. 159. — Hypertrophy of tissues about the pycnia and aecia: *A Gymnosporangium juniperi-virginianae* on leaf of apple, *B Spirechina loeseneriana* on leaf of Rubus; *p* pycnia, *a* aeciospores, *d* peridium. (*A* after Reed & Crabill, 1915; *B* after Stämpfli, 1910.)

phenomena observed in connection with the rusts (p. 36).

Hypertrophy is often brought about in some degree by the massing of hyphae between the cells of parenchyma, and is especially observable in the gametophytic stage of the rust. A more definite hypertrophy

is a common accompaniment of localized aecia in the species of many genera. Often it is only the epidermal cells immediately surrounding the aecium that are swollen, (Fig. 74), but more frequently the neighboring parenchymatous cells are also affected. The result is the same both with ordinary aecia of whatever form (Fig. 159 *A*) and with stylosporic aecia (159 *B*), and is determined rather by the nature of the mycelium than by the kind of sorus.

When numerous points of infection are sufficiently close together so that the infected areas coalesce, and especially when in connection with active meristematic tissues, a pronounced hypertrophy results, often accompanied by much distortion. The great difference in the amount of swelling between isolated infection in the blades of thin, nearly mature leaves and that in young leaves, petioles and stems, is well shown by the aecia of *Puccinia caricis* on Urtica, *P. sambuci* on Sambucus, *P. fraxinata* on Fraxinus, *P. rivinae* on Rivina (Fig. 160), *P. arrhenatheri* on Berberis, *P. rubigo-vera* on Clematis (Fig. 161), and many other instances, in which gametophytic mycelium gives rise to the common form of aecia.

Fig. 160. — Shoot of *Rivina octandra* distorted by aecia of *Puccinia rivinae*. (After Arthur & Johnston, 1918.)

Examples of the same abnormal changes are also found among microcyclic species, *e.g.*, *Puccinia obliqua* on Funastrum and *P. ruebsaamenii* on Origanum, where again the mycelium is gametophytic.

There appear to be no instances of hypertrophy of a similar nature arising from sporophytic mycelium, although sometimes such mycelium may occasion fusiform swellings of woody stems, as *Puccinia splendens* on Hymenoclea, and *Gymnosporangium clavariaeforme* on Juniperus, or produce round woody galls, as with other species of Gymnosporangium.

When the infection takes place in a bud or growing point, the rust becomes systemic, and a different form of hypertrophy ensues. The

shoot which arises from the bud usually forms elongated internodes with much reduced leaves (Fig. 162) and never comes to fruition, although it sometimes bears abortive and much distorted flowers (Fig. 163). Instead of a single shoot from an infected bud, many shoots may arise, thus forming a witches' broom (p. 311). Whether the shoots

Fig. 161. Hypertrophy of stem and leaves of *Thalictrum flavum* by the aecia of *Puccinia rubigo-vera tritici* (*P. triticina*). (Original, photograph by Mains.)

are single or multiple, simple or branched, they usually fail to produce chlorophyll and assume an etiolated appearance, but only when associated with gametophytic mycelium. The hypertrophy arising from bud infection is usually combined with a certain amount of hypoplasia, showing prominently in the atrophied leaves.

Galls. — When a marked hypertrophy occurs in an organ and especially when the swelling is circumscribed and more or less abrupt, it is designated as a gall. Galls are fusiform, globoid, or lobed in form, annual or perennial in duration, and occur either on herbaceous or woody parts of a plant. The tendency to form galls is partly inherent in the character of the tissues invaded *e.g.*, when *Puccinia rubigo-vera*

produces galls on succulent organs of Clematis, Thalictrum, etc., although usually only producing aggregate swellings on these hosts, and partly in the specific nature of the rust, *e.g.*, *Gymnosporangium juniperi-virginianae* (Fig. 164) and *Cronartium cerebrum*. The latter species produces as a gametophyte two caulicolous forms of galls. When the infection occurs on the trunks or branches of *Pinus taeda* or *P. palustris* the galls are spindle-shape (Fig. 165 *a*), when on *P. rigida*, *P. echinata* or *P. virginiana* the galls are globoid (Fig. 165 *b*). There is also a form of this species on cones. These marked differences in form may be

Fig. 162. — Systemic invasion of the shoots of *Tithymalus cyparissias*, with much reduced leaves and greatly elongated internodes: at the upper part the shoots have outgrown the mycelium and have regained their normal habit. (After Tischler, 1911.)

Fig. 163. — Modified inflorescence of *Tithymalus cyparissias* by systemic invasion of *Uromyces pisi:* all the flowers are abortive. (After Stämpfli, 1910.)

due to host reactions, or they may represent different strains, or possibly different species of rusts (Arthur, 1907–27, p. 602), although distinct diagnostic characters of a morphologic nature have not been noted. A parallel case is that of *Cronartium harknessii* in the western United States which has three caulicolous forms of aecia (Arthur, 1907–27, p. 695), while a nearly parallel case is that of *C. comptoniae*,

which produces slight swellings on *Pinus rigida* but numerous small galls on *P. virginiana.*

Systemic infection. — When the mycelium of a rust pervades all the organs in a definite part of a plant, or in the whole plant, it is described as systemic. Such behavior of the mycelium with a few exceptions, as in Calyptospora and certain species of Gymnosporangium, is

Fig. 164. — Telial galls of *Gymnosporangium juniperi-virginianae* on *Juniperus virginiana,* before the pedicels of the spores have elongated and become gelatinized. Compare with Fig. 179. (Photograph by Reed & Crabill.)

Fig. 165. — Two gall forms of *Cronartium cerebrum* on the trunks of young pines: *a* spindle form (*Peridermium fusiforme*) on *Pinus taeda, b* globoid form (*P. cerebrum*) on *Pinus echinata.* (After Hedgcock & Long, 1914.)

only shown in the gametophytic phase. It is a characteristic feature of diagnostic value in such species as *Puccinia eatoniae* on *Ranunculus abortivus, P. monoica* on Arabis and related genera, *P. epilobii-tetragoni* on various onagraceous genera, *Uromyces plumbarius* which is correlated with the last species, *U. carneus* on Astragalus, *U. porosus* on Vicia, *U. pisi* and *U. occidentalis* on Tithymalus, *Tranzschelia punctata* and *Ochropsora sorbi,* both on Anemone, *Melampsora arctica* on Saxifraga, and many other species of macrocyclic rusts. It also occurs in many microcyclic species, as *Puccinia holboellii* on Arabis and *Uromyces tranzschelii* on Tithymalus. Systemic infection results from the ability of the mycelium to penetrate the meristematic tissues near or at the growing point of the stem and to follow up the growth of the organ as development progresses. It is marked by hypoplastic changes, the leaves usually being smaller and chlorotic and the stems and petioles

more or less drawn (Fig. 162). The most striking effect of systemic infection is shown when adventitious buds are stimulated into growth and witches' brooms are formed.

Witches' brooms. — One of the best known and most widely distributed kinds of witches' brooms, is that of *Melampsorella elatina* on Abies. It occurs in Europe, northern Asia, Japan and North America, and may be taken as a typical example of this sort of malformation. It is the result of infection in a growing point. The parasitic fungus penetrates the meristematic tissues and induces an active development of both lateral and supernumerary buds. These groups of buds extend into much branched and negatively geotropic stems, bearing reduced leaves, and altogether forming a somewhat compact, oval mass, ranging between 20 and 50 cms. in height, or sometimes more. The entire growth is devoid of chlorophyll, which makes it a conspicuous object against the dark green of surrounding foliage. The leaves drop at the close of the growing season like those of deciduous trees (Fig. 166). Witches' brooms of this species are usually tinged with pink, but the very similar American form on Picea, *Peridermium coloradense*, is a clear pale-yellow. The alternate stage of the latter form is not known, although it has been asserted to be identical with the preceding (Weir & Hubert, 1918), but this seems improbable from the unlike formation of the pycnia. The age of witches' brooms of this character is naturally limited by the absence of chlorophyll. The annual rings at the base of a large witches' broom on Abies were counted (de Bary, 1863a) and indicated a period of growth of sixteen years, but similar chlorotic witches' brooms on other hosts are much shorter lived, depending largely on the natural life of the host. Those on Rubus caused by *Gymnoconia interstitialis* (Fig. 167) persist only a few years, and those on the annual Chamaesyce caused by *Uromyces proëminens* (Fig. 154) terminate with the death of the host, or even before.

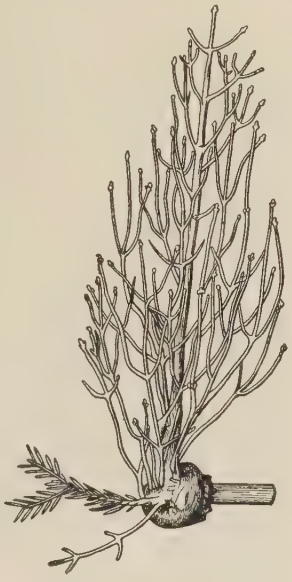


Fig. 166. — Witches' broom on *Abies pectinata* caused by aecia of *Melampsorella elatina* in the leafless winter condition. Observe the upright growth from the gall-like swelling. (After Hartig, 1900.)

Chlorotic witches' brooms, whether on hosts that are annual or

perennial, herbaceous or woody, are all produced by gametophytic mycelium, and are induced by rusts belonging to various genera, which are both macrocyclic and microcyclic. *Caeoma deformans* on *Thujopsis dolabrata* in India is apparently a macrocyclic form although its alternate host is not known. Another rust on trees of the same nature, but microcyclic, is *Uromycladium tepperianum* which is conspicuously abundant on various species of Acacia in Australia and Tasmania. *Cronartium jacksoniae* is another microcyclic rust forming witches' brooms in Australia. It attacks leguminous shrubs belonging to a number of genera. Various shrubby species of Rubus in North America form witches' brooms when infected with basidiospores of *Gymnoconia interstitialis* in the buds (Fig. 167) and occasionally through wounds in the roots (Dodge, 1923c). The microcyclic form of the same rust (*Kunkelia nitens*) also produces similar witches' brooms. When the meristematic tissue of the rapidly growing buds of certain twining plants are parasitized pronounced distortions resembling witches' brooms are formed, as with the macrocyclic rust, *Puccinia rivinae* on species of Rivina in tropical America, (Fig. 160) and the microcyclic *P. obliqua* on various hosts belonging to the Asclepiadaceae.

Fig. 167. — Witches' broom on cultivated blackberry, two years old, produced by *Gymnoconia interstitialis*. Such shoots are much paler than normal. (After Dodge, 1923c.)

Witches' brooms produced by sporophytic mycelium are similar in their development both in form and size to those produced by gametophytic mycelium but do not exhibit chlorosis. They retain the natural color of normal shoots, and are conspicuous only by the compact growth of many slender branches. The best known and most investigated

example is that of *Calyptospora columnaris* on Vaccinium (Fig. 168), whose aecia on Abies produce little or no disturbance of the host except yellowing of the infected leaves. The sporophytic stage occurs on various species of Vaccinium, which are all shrubs ranging from two to ten decimeters in height. Usually only one or two witches' brooms occur on an individual shrub, and may attain a size of two by three decimeters. The leaves of the infected shoots are smaller or even wanting, but are not noticeably changed in shape or color. The stems are evenly swollen by a uniform distribution of telia and resemble polished brown pipe-stems.

FIG. 168. — Sporophytic witches' broom of *Calypiospora columnaris: A* on *Vaccinium pennsylvanicum*, *B* detail of swollen stems. (*A* original; *B* after Frank.)

The largest and most noticeable sporophytically produced witches' brooms occur on the Cupressineae, and are caused by species of Gymnosporangium. Like those of Calyptospora they are non-chlorotic. Probably the finest examples are due to *G. juvenescens* (Fig. 169) and *G. kernianum*, although those produced by *G. nidus-avis* and *G. ellisii* are sometimes as large, but lack the regular formation. All gradations exist between the proliferating infection of meristematic tissue in buds and the more or less local and scattered infection of other parts of the same hosts, so that witches' brooms and scattered infection may often occur on the same tree from the same species of rust, a phenomenon which is much more rare with gametophytic growths.

GEOTROPIC RESPONSE. — Whenever the mycelium invades the growing point of the stem, or a lateral bud, whether it be gametophytic or

sporophytic in character, a change takes place in the reaction to gravity. Whatever may be the normal direction of growth the axes now become orthogeotropic and the leaves assume a uniform plagiogeotropic position. This change in direction of growth is well illustrated in the witches' brooms on Abies (Fig. 170). The normal lateral branches of Abies assume a more or less horizontal position while the branches of the

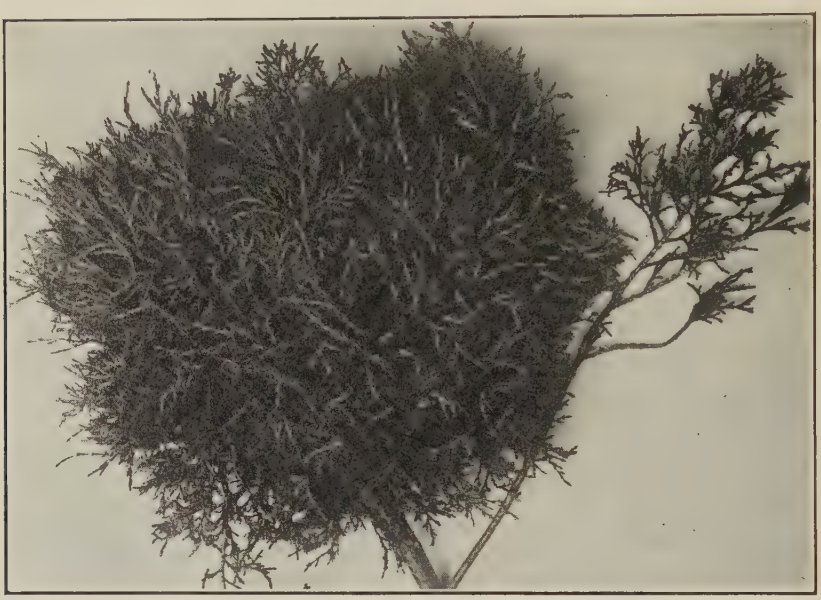


FIG. 169. — Sporophytic witches' broom of *Gymnosporangium juvenescens* on *Juniperus scopulorum*, with a normal shoot. (Kern, 1911, photograph by E. Bethel.)

witches' broom grow upright, and in this regard are like the normal terminal shoot. The leaves on the normal lateral shoots of Abies assume a horizontal position, and by twisting their bases they come to lie in two rows. The leaves on the diseased stems, however, stand out in all directions equidistantly disposed, like the leaves on the terminal shoot. The histologic features of the diseased portion also correspond more nearly to those of the healthy terminal shoot (Anderson, 1897). The same change in direction of growth is prominent in Chamaesyce infested with *Uromyces proëminens* (Fig. 154), and is shown to a greater or lesser degree by all organs when systemically invaded by a rust, *e.g.*, in the woody stems of Abies, and in the leaves of Hepatica (Fig. 153).

Rejuvenescence. — A marked feature of systemic invasion by a rust is the assumption of juvenile characters in the host. Probably it would be more accurate to say that the fungus inhibits the changes in the host that accompany normal ontogenetic development. This is well shown in the witches' broom on Abies, which in its gross and microscopic morphology and in its sensitiveness to stimuli resembles the normal terminal shoot, which in turn retains the characteristics of the central axis of the seedling. Certain species of Gymnosporangium on Juniperus of the section Sabina, the red cedars, illustrate this kind of inhibition in a striking manner. *Juniperus virginiana, J. scopulorum,* and *J. horizontalis* have mature foliage with scale-like blunt appressed leaves, while leaves of the young plants are subulate, spiny-tipped and spreading. Although the witches' brooms which these hosts bear, *e.g., G. nidus-avis* and *G. juvenescens,* arise from branches on trees of many years' growth, yet the foliage of the witches' brooms wholly or in large part assumes the juvenile form (Kern, 1911).

Fig. 170. — Small witches' broom on *Abies pectinata* caused by aecia of *Melampsorella elatina,* showing normal horizontal position of a healthy branch and vertical growth of the diseased branches. (After Tubeuf, 1897.)

The modification in form of leaves and the deformation of flowers are common phenomena in connection with gametophytic infection in the crown of herbaceous plants. In general the effect is to reduce the size and simplify the form, of which the well known change in leaves of Hepatica by *Tranzschelia punctata* is a good example (Fig. 153). The action upon flowers has been studied especially in *Uromyces pisi* (Stämpfli, 1910; Tischler, 1911). This rust and a number of similar species attack several species of Tithymalus and in every instance the flowers are partly changed in the direction of foliage leaves, are wholly so changed, or are entirely suppressed (Fig. 163).

When the mycelium of a rust penetrates the meristem of a growing point not only is the direct action of the rust shown in the external morphology of the invaded portion of the host, but all the tissues are

more or less retarded or advanced in their usual transformations. This action produces a larger proportion of parenchyma or parenchyma-like cells than in normally developed organs. Many of the wood and bast elements, together with the collenchyma and other strengthening tissues, fail normally to thicken the walls of their cells. In consequence the osmotic pressure within the cells causes them to become shorter and broader. In these and other ways the parasite, when in contact with the strongly nascent tissues of the host, changes the normal course of development.

ANATOMIC CHANGES IN THE HOST

Whatever disturbs orderly ontogenetic growth is likely to distort the organs and tissues in a definite way, varying with the disturbing agent. When the mycelium of rusts is confined to parenchymatous tissues the changes in the organ are mostly brought about by stimulation, or more rarely repression, in the growth of the cells of the parenchyma, but when the fibrovascular bundles are invaded the several elements of the entire organ are affected, but not to an equal degree.

It is worthy of note that in all the anatomic changes induced by the rusts there is rarely any formation of wound tissues, or layers of cork (p. 318) or callus, or any marked traumatic response indicating the presence of a foreign body. The rust acts when in congenial hosts as a symbiotic organism, whose demands on the host may be at times in excess of available resources.

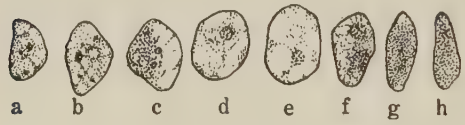


Fig. 171. — Changes in nuclei of host induced by presence of *Puccinia graminis tritici: a* normal nucleus from uninfected tissue; *b, c, d* progressive enlargement of both nucleus and nucleolus in a seven-day infection; *e* maximum size in ten-day infection; *f, g, h* progressive collapse. (After Allen, 1923b.)

The presence of the rust mycelium in the tissues of the host does produce, however, at least in the earlier stages, a certain amount of stimulation which is manifested partly by increased turgor causing enlargement of individual cells and tissues and partly by enlargement of the whole organ. Even when none of these effects is observable there may be induced an increase in size of the nuclei (Fig. 171). This has been recorded for *Puccinia rubigo-vera secalis* on rye and *P. graminis avenae* on oats (Eriksson, 1904, 1905), for *P. graminis tritici* on wheat (Allen, 1923b), for *P. coronata* on oats (Ruttle & Fraser, 1927), and for *P. violae* (Reynolds, 1912). With *P. violae* even two or three enlarged nuclei are sometimes formed in a cell, all more or less distorted.

There may also be an increase in the number of nucleoli. In the galls of *Gymnosporangium juniperi-virginianae* sometimes even thirty per cent of the cells are binucleolate (Reed & Crabill, 1915). Such results are clearly due to abnormal stimulation induced by the presence of the mycelium of the rust.

A variety of changes occur in the cells. Parenchymatous tissues are the ones most readily and conspicuously altered. In these the cells become much larger and by crowding obliterate the intercellular spaces. Not infrequently a marked increase in the number of cells takes place. The irregular mesophyll cells of the leaf tend to become globoid, and when much compacted are angular. When such cells are stretched in one direction by osmotic pressure, as often occurs in the formation of aecial swellings on leaves, they may simulate palisade cells, but are usually larger and less regular (Reed & Crabill, 1915).

The palisade cells of leaves, when they are affected, usually show the same tendency to become isodiametric as do the mesophyll cells, and the number of layers may either increase or diminish.

The pith cells of the stem or petiole follow the same tendencies as those of the foliar mesophyll. Sometimes they increase to an extent which forces them through the vascular and cortical rings and in this way produce excrescences (Fig. 172), as with *Aecidium englerianum* on Clematis (Lindau, 1893) and *Spirechina loeseneriana* on Rubus (Stämpfli, 1910).

The vascular elements become variously changed under the influence of the parasitic mycelium. These changes vary in reaction to the different species of rusts and even for different hosts with the same species of rust. In general the tendency to produce shorter, broader and thinner walled cells for each element both in leaves and stems is marked, and especially in galls (Stämpfli, 1910) and witches' brooms (Anderson, 1897). As growth proceeds and the gall enlarges the several elements of the stem or leaf lose their usual orderly arrangement and are variously displaced.

The fibrovascular ring is usually irregularly broken up and comparatively reduced by the enlargement of the medullary rays, which latter, like the pith and the cortical parenchyma may increase the number and size of their cells (Stämpfli, 1910). The bundles of tracheids and bast fibers are sometimes more numerous, but of indefinite position (Harshberger, 1902; Stewart, 1915). In general the strengthening tissues are weakly developed. Woody galls, especially those in coniferous hosts, secure their bulk not only by the great increase in parenchymatous

elements but to a lesser degree by multiplication of the elements in the phloëm and xylem, in which the walls of the cells are sometimes unduly thickened. In galls on *Pinus rigida* induced by *Cronartium cerebrum* frequently "about twice as much wood is formed in the diseased region as in the healthy" (Dodge & Adams, 1918). Resin ducts are generally larger, but with the strengthening cells about the epithelium absent or weak (Anderson, 1897).

The epidermis, as a rule, is less modified than the other tissue elements. The cells sometimes are enlarged but quite as often are smaller. In the

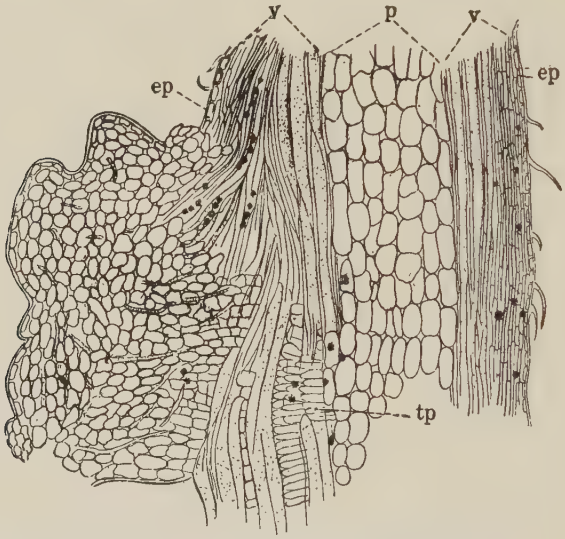


Fig. 172. — Longitudinal section of a gall on the shoot of *Rubus brasiliensis:* the tissue of the pith is forced through the vascular ring; *ep* epidermis, *v,v* vascular ring, *p* pith, *tp* pith cells elongated transversely and pushing through the vascular ring to form the gall. (After Stämpfli, 1910.)

cedar-apple gall of *Gymnosporangium juniperi-virginianae* the epidermis over the gall is replaced by a cork-like layer, four to six cells thick (Sanford, 1888; Reed & Crabill, 1915). Trichomes are generally reduced in number or absent. On the galls of *Spirechina loeseneriana* trichomes are absent, although present on normal tissues (Stämpfli, 1910), while on the witches' brooms of *Melampsorella elatina* the trichomes are absent, or small and one-celled, agreeing in this regard with the normal terminal shoots of the host, *Abies balsamea*, but not with the normal lateral shoots, which bear numerous long trichomes (Anderson, 1897). The number and position of stomata are rarely changed by

the presence of a rust, but the leaves of Rubus invaded by *Gymnoconia interstitialis* form numerous stomata on the upper surface while the normal leaves bear very few or none, yet the under surface of both normal and diseased leaves are plentifully supplied with stomata (Dodge, 1923e). This development is in contrast to the gall formed on Rubus by *Spirechina* on which stomata are entirely absent (Stämpfli, 1910).

PHYSIOLOGIC DISTURBANCES IN THE HOST

The changes which take place in the normal activities of the living cells of a host when invaded by the mycelium of a rust are manifested in many ways. Some of the more prominent deviations include the processes of transpiration, respiration, photosynthesis, and variation in cell contents of chlorophyll, starch, calcium oxalate and diffusible products.

Transpiration. — Little exact information is available bearing upon the influence of the fungus on the transpiration of the host. It is usually assumed that the loss of water through the open sori of diseased tissues materially adds to the normal transpiration. There are some data to support this opinion. In an experiment with leafy branches of Rubus permeated with the gametophytic mycelium of *Gymnoconia interstitialis* the cut ends of both diseased and healthy branches were placed in water. The diseased branches, although they absorbed nearly twice as much water as the healthy branches, yet failed to become turgid, apparently due to excessive evaporation (Blodgett, 1901). A decided increase in transpiration occurs in leaves of *Pinus virginiana* invaded by *Gallowaya pinicola*, which is ascribed in large part to the rupture of the epidermis by the sori (Galloway, 1896). Tests were made by using branches and also single leaves. When the infected part of a leaf was cut away the transpiration of the remaining portion was normal.

Uredinial infection of wheat, rye and oats with *Puccinia graminis*, sunflower with *P. helianthi*, and carnation with *Uromyces caryophyllinus*, in an extensive series of experiments (Weaver, 1916) gave a consistent increase in transpiration of the diseased over the healthy plants, amounting to more than double the normal rate when the rust covered the whole leaf area. The increase began to show about the time that the uredinial sori broke through the epidermis, and was approximately proportional to the number of sori involved. This relationship was so close that an increase of 0.2 to 0.3 per cent in the total area of the open sori was registered by a definite increase in the transpiration rate. After new sori ceased to appear the rate of transpiration remained prac-

tically constant. In a similar test with cocklebur (Xanthium) bearing the microcyclic rust, *Puccinia xanthii*, a decided decrease in rate of transpiration was noted. This rust possesses a compact sorus which may not permit ready movement of moisture.

The number of stomata is greatly increased on the upper surface of systemically infected leaves in some instances, *e.g.* Rubus bearing *Gymnoconia interstitialis* (Dodge, 1923e) and Tithymalus bearing *Uromyces pisi* (Tischler, 1911), but whether such stomata are active or not during the time the sori are open has not been recorded. Apple leaves bearing aecia of *Gymnosporangium juniperi-virginianae* have the substomatal cavities obliterated on the infected portions of the leaf, and the stomata themselves may be functionless and remain partially open both day and night. The transpiration of such leaves is found by experiment to be much greater during the nighttime than that of healthy leaves, although less in the daytime, presumably because healthy leaves have the ability to regulate the amount of transpiration through the stomata, while this power is almost lost in the diseased leaves (Reed & Crabill, 1915). The conclusion from the available data appears to be that in general the active mycelium of a rust stimulates transpiration, while at the same time checking its expression by choking up the intercellular spaces and substomatal cavities, and by rendering the stomata functionless. The large amount of moisture that can escape through certain loosely formed sori, *e.g.*, uredinia, can be readily detected, but so little escapes through other compact sori that it can be detected only when active stomata are closed by darkness.

Respiration. — Extensive data on respiration, or the exchange of oxygen and carbon dioxide, in rust-diseased plants are derived from experiments by Reed and Crabill (1915), conducted during 1913 and 1914. They took the amount of carbon dioxide exhaled as an index of respiration. Leaves of apple bearing aecia of *Gymnosporangium juniperi-virginianae* were compared in 1913 with healthy leaves gathered at the same date using a Ganong respirometer in a dark chamber. Leaves taken in July before aeciospores began to be discharged, showed an average of about 20 per cent respiration above that of healthy leaves, while after the spores began to be discharged the respiration fell to about 12 per cent above the normal. The observations were made over a period of about two months. More detailed experiments were conducted in 1914 using both the Ganong respirometer and a modified Sachs apparatus, but this series included no tests made prior to the time when aeciospores began to be shed. The results of all the tests, of which

there were 170 recorded, show that diseased leaves respire more, usually much more rapidly than healthy leaves. In about 15 hours the diseased leaves usually ceased entirely to produce carbon dioxide, while healthy leaves usually continued to do so for 48 hours or more. When the test was run sufficiently long the amount of carbon dioxide exhaled was about the same for both diseased and healthy leaves. It is evident that in the dark the store of oxidizable substances soon becomes exhausted, while with the usual exposure to daylight diseased leaves continue to be supplied with oxidizable substances to the capacity of their reduced area of green tissues. If it be assumed that respiration is an index to the amount of metabolism, the presence of the rust clearly speeds up the metabolic processes, at least in the earlier stages of its development, and at the same time lowers the total available energy of the host.

A test of wheat plants heavily infected with *Puccinia graminis* (Bailey & Gurjar, 1920), taken about two weeks before full maturity, gave not much more than half the carbon dioxide obtained from healthy plants. In this experiment whole plants from above ground were placed in sealed tubes in the dark for 24 hours, and the respired carbon dioxide determined. In interpreting this result it must be borne in mind that the plants were nearly at the end of their period of growth, and that the rust had reached a stage of greatly restricted development. This is indicated both by a reported 10 per cent deficiency in total moisture and by a slightly heavier weight of the (prematurely ripened) dried grains. Therefore, the lessened respiration of the diseased plants must have been due to a reduced amount of oxidizable material (for which no data were secured), and indicated the heavy drain the parasite had exerted upon the host during the period of growth. This interpretation is also supported by an inspection of the data supplied by Reed and Crabill (1915), showing a greatly decreased respiration of apple leaves infected with *Gymnosporangium juniperi-virginianae* in the latter part of the season for growth.

Experiments on the respiration of the hosts of seven species of rusts, *viz.*, *Puccinia smyrnii*, *P. malvacearum*, *P. kundmaniae*, *Phragmidium subcorticium*, *Phr. rosae-sempervirentis*, *Melampsora pulcherrima* on Mercurialis and *Tranzschelia punctata* on Anemone (Nicolas, 1920), gave in every instance a greater exhalation of carbon dioxide for diseased plants than for healthy ones. The conclusion is drawn that "the respiratory intensity of parasitized organs is higher than that of healthy organs."

In the several experiments to which allusion has been made only one systemic rust was included, *i.e.*, *Tranzschelia punctata* on *Anemone coronaria*. While this rust agrees with all the others reported in showing a greater intensity of respiration, it differs from the others in the far greater amount of oxygen required during the process. The significance of the observation, if it should be verified in other instances, is not apparent.

Photosynthesis. — The presence of either the gametophytic or sporophytic mycelium among the tissues of a host acts to decrease the amount of chlorophyll in the cells, or even entirely to inhibit its formation, except in a few restricted instances, *e.g.*, "green islands" (p. 305). This loss of chlorophyll is readily detected by the yellowing of the affected parts. As the photosynthesis of a plant depends upon the presence of chlorophyll in conjunction with light, it is a logical conclusion that decrease in the normal production of chlorophyll will lead to a decrease in the amount of carbon dioxide absorbed and oxygen given off by the diseased tissues. Experimental confirmation of such detrimental action by the aecia of *Gymnosporangium juniperi-virginianae* in apple leaves has been provided by Reed and Crabill (1915). It was found by using a Ganong photosynthometer that the photosynthesis of diseased leaves, using the amount of carbon dioxide consumed as a measure, was much depressed, varying from 56 to 65 per cent as an average for the ten weeks following the first week in July. A chemical analysis of the healthy and diseased leaves disclosed a corresponding loss in sugars and starch. Similar results have been obtained (Long, 1919) by using the leaves of oats bearing uredinia of *Puccinia coronata*, when the photosynthetic activity dropped from 72 per cent in the earlier stages of the rust to 48 per cent in the pustular stage. A comparison of the infected with the non-infected areas of the same leaf showed only 21 per cent as much photosynthate in the former. Similar results by the same experimenter were obtained with uredinia of *Puccinia graminis* on wheat and aecia of *Uromyces caladii* on Arisaema.

The decrease in photosynthetic activity in the host is reflected in the development of the parasite. The incubation period may be retarded (Fromme, 1913; Mains, 1917), or the development wholly checked (Ward, 1903a), by the absence of light for a shorter or longer period. Etiolated plants, *i.e.* those in which chlorophyll formation is inhibited due to the absence of light, are difficult to infect (Stakman & Piemeisel, 1917), as many investigators have found.

Chlorophyll. — One of the most conspicuous symptoms produced

by rusts is the paling or yellowing of infected tissues, particularly of leafy organs. These changes have been noted by many workers when engaged in cytologic studies. All gradations of chlorophyll loss are to be discerned in the infected areas. In general the loss is most pronounced at the center of infection and fades away more or less gradually into the surrounding healthy tissues. Not only may the chlorophyll pigment be lost but the plastids are frequently destroyed in part or wholly.

In systemic invasion of an organ by gametophytic mycelium, *e.g.*, *Melampsorella elatina* on Abies, *Gymnoconia interstitialis* on Rubus, etc., no data are available to show how completely the production of chlorophyll is inhibited, but in many instances seemingly little if any is formed.

The production of chlorophyll under the stimulation of the rust mycelium on the other hand is a notable occurrence in such instances as "green islands" and its analogous appearance in normally colorless organs (p. 306).

Starch. — In many instances an abundance of starch has been detected in the tissues of various plants invaded by the gametophytic mycelium of different rusts (Barclay, 1887; Wakker, 1892; Fentzling, 1892; Clinton, 1893; Tubeuf, 1897; Halsted, 1898b; Colley, 1918). This production of starch is associated with the preliminary growth of the fungus.

In the microcyclic species, *Chrysomyxa abietis* on Picea, during the first season after infection, an abundance of starch is stored in the diseased tissues, which entirely disappears the next spring during the formation of the microteliospores (Tubeuf, 1897). The same behavior has been noted in *Melampsoropsis pyrolae*, in which large quantities of starch occur in connection with the uredinia. The uredinial mycelium hibernates in the rootstock and makes a systemic invasion of the young leaves in early spring. With the formation of telia on the same leaves about two weeks later the starch disappears (Rice, 1927). The same relation is shown in galls of *Gymnosporangium juniperi-virginianae*, in which starch is plentiful up to the time the teliospores begin to form, after which it rapidly disappears (Reed & Crabill, 1915). What part the rust has in the production of starch is not apparent. There is, however, a clear association of the increased quantity present during the early growth of the rust and its disappearance in the later stages of development.

Some isolated records remain to be mentioned, which require further information. Leaves of apple bearing *Gymnosporangium juniperi-vir-*

ginianae were chemically analyzed and gave less starch than healthy leaves (Reed & Crabill, 1915). The analyses were made in August and there are no data for the condition earlier in the season. Corn (maize) plants bearing uredinia of *Puccinia sorghi* have been found to be without starch in the invaded areas (Mains, 1917; Rice, 1927), and the same is recorded for *Spirechina loeseneriana* on Rubus (Stämpfli, 1910).

Calcium oxalate. — By-products of cell activity are sometimes absent and sometimes occur in extra abundance in connection with the growth of rusts. A total lack or diminished amount of calcium oxalate has been noted in Rhamnus with *Puccinia coronata*, Urtica with *P. caricis*, Sanguisorba with *Xenodochus carbonarius*, Crataegus with *Gymnosporangium clavariaeforme* (Wakker, 1892), and Phyteuma with *Uromyces phyteumatum* (Stämpfli, 1910), while an increased amount has been found in Rubus with *Spirechina loeseneriana* (Stämpfli, 1910) and pear with *Gymnosporangium sabinae* (Fentzling, 1892).

Other substances. — In connection with the invasion of rust mycelium there may occur resinous or fatty substances (Adams, 1919), superabundant secretion from an increased number of resin ducts in coniferous woods, various coloring matters, especially anthocyanin in such plants as corn (maize) attacked by *Puccinia sorghi* (Rice, 1927), and sorghum bearing *P. purpurea*. Such by-products are mostly or wholly due to a disturbance in normal function, and are not dependent upon a particular parasite or host but may be induced by almost any kind of injury under special conditions.

PATHOLOGIC INJURY TO ANIMALS AND MAN

Injury to animals. — Toxic qualities in *Puccinia xylorrhizae* have been suspected in connection with annual death of sheep on the ranges in Wyoming. This rust occurs in abundance on the woody aster, *Xylorrhiza parryi*, native of the region. The host has been proved by experiment to be poisonous to sheep, and "the presence of the fungus may add to the poisonous character of the plant" (Prien & Raiford, 1911). This suspicion was warranted by circumstantial evidence, but later studies have proved it to be erroneous.

Heavily rusted wheat straw has been eaten by farm animals with none but salutary effect (Snyder, 1905). The young hypertrophied galls of various Pucciniaceae are often eaten and relished by children. Those of *Puccinia caricis* on Urtica are utilized as food by the Himalayans (Gwynne-Vaughan & Barnes, 1927). It is probable that no

member of the rust family, when eaten, possesses toxic properties injurious to animals or man.

Suspicion has also been directed toward the clover rust (*Uromyces trifolii*), as capable of inducing severe irritation and even ulceration in the stomach of cattle.[1] Again, however, direct proof has not been obtained.

Injury to man. — Hay fever and asthma are known to arise from pollen grains, and it is not unlikely that these diseases may sometimes be induced by the urediniospores of rusts, especially those of the cereals. A positive case of asthma has been recorded (Cadham, 1924), in which the evidence strongly pointed to the rust of wheat and oats (considered to be *Puccinia graminis*) as the causal agent. In this case, which occurred in Manitoba, "a whiff of a few rust spores was sufficient to induce a paroxysm." The patient received some relief from vaccine prepared from urediniospores of wheat rust. The etiologic factor was further indicated by positive cutaneous reaction.

In a letter dated February 25, 1928, additional information is supplied by the same investigator. The cutaneous reactions of two patients suffering from asthma were equally pronounced with the urediniospores derived from *Puccinia graminis* on wheat, barley and rye, and from *P. rubigo-vera tritici*. Serologic tests gave no material differences between the various grain rusts employed. Doubtless the spores of any of the grain rusts are likely to be pathogenic to susceptible persons. As the air is often laden with urediniospores in the vicinity of grain fields, especially at harvest time, such a source of infection is often highly probable.

[1] Mohler, J. R. Mycotic stomatitis of cattle. Circ. Bur. Animal Indus., U. S. Dep. Agr., 51. 6 pp. 1904.

CHAPTER IX

ECONOMIC CONSIDERATIONS

Cereals and grasses: stem rust on wheat, oats, rye, timothy; stripe rust; leaf rust on wheat, oats, rye, barley, corn, sorghum.
Fruit trees: apple, in eastern United States, in Japan and China; pear and quince, in United States, in Europe, in the orient; stone fruits; fig; coffee.
Small fruits: raspberries and blackberries, orange rust, yellow rust, late rust, cane rust; currant and gooseberry; grape.
Vegetable crops: asparagus; bean; pea; beet and spinage; peanut.
Forage crops: clover; alfalfa; cowpea; sunflower.
Ornamental plants: snapdragon; carnation; chrysanthemum; hollyhock; rose.
Fiber crops: flax; cotton.
Forest trees: pine; fir; spruce; hemlock; larch.

The rusts are fungi of great economic importance. While they attack nearly all kinds of plants, the most destructive diseases and the greatest economic losses occur among cereals, fruits, vegetables, forage, fiber and ornamental crops, and forest trees. Some kinds that have proved most injurious are considered in the following pages.

THE RUSTS OF CEREALS AND GRASSES

The rusts which attack cereals (wheat, rye, oats, barley, corn, etc.) and various grasses are among the most important of all the rusts from the economic standpoint. This is due in large part to the fundamental value of these crops, which form the basis of the food supply of the world, and to the wide-spread and aggressive nature of the rusts involved. While the cereal rusts have received more intensive study on the part of plant pathologists than the rusts of any other group of crop-plants, no method has yet been found wholly to prevent enormous losses.

There are six important rusts of the small cereals. One of these, *Puccinia graminis*, is known as stem rust, because it usually attacks the culms and sheaths. The others attack the blades of the leaves chiefly, and are collectively known as leaf rusts. The stem rust has long been considered the most injurious of the rusts. It was the first to be recognized as a source of economic loss, being known as such for

centuries before the Christian era (pp. 32–34), and has become the embodiment of the collective idea of all rusts in the public mind.

Due to the long period in which attention has been directed toward the stem rust it has naturally received more intimate study than the leaf forms. The relative importance of the latter has been generally underestimated, and not until recently have the injuries which they cause been properly appreciated by growers, agronomists, and plant pathologists.

Rusts do not appear in uniform abundance year after year, but depending upon the weather and other factors, partly unknown, they vary from an inconspicuous amount in some years to an epidemic form in others, so that it is common to speak of certain seasons as "rust years." Of course, the more conspicuous stem rust of wheat and rye is usually the one to be understood, although in central Germany and eastward, where stripe rust, one of the leaf forms, is usually most destructive, that may be the one intended.

Jethro Tull[1] has recorded that in England the year 1725 produced rust, "the like never having been heard of before." Sir Humphrey Davy (1814) said that rust was very destructive in 1804. In Germany 1891 was a "rust year," and in Bavaria, 1911 (Esmarch, 1926). In Australia 1903 proved a very destructive year for rust.

Fig. 173. — Normal (*a*) and shrunken (*b*) kernels of wheat, showing the effect of stem rust upon the yield. (Photograph by C. T. Gregory.)

But the greatest "rust year" of world wide extent was undoubtedly 1916, and to indicate this a few figures will suffice. In western Australia the loss is estimated to have reached £2,000,000 ($10,000,000), in Saxony M47,000,000 ($12,000,000) in western Canada $100,000,000, and in the upper Mississippi Valley (Iowa, Minnesota and the two Dakotas) $115,000,000. All these estimates refer to the stem rust on wheat alone. So great was the injury that thousands of acres of wheat were never garnered; the yield would not have paid for the labor and materials used in harvesting. Not only is the yield of grain reduced, but the kernels formed are often shrunken (Fig. 173) and of inferior quality.

[1] Tull, J. Horse-hoeing industry. Ed. by William Corbett, 466 pp. 1729.

Taking into account all grain growing countries the annual loss in the cereal crops is estimated by Eriksson to be some M1,250,000,000, or over $300,000,000. During the ten-year period, 1915–1924 inclusive, there was a loss from stem rust in wheat alone in thirteen states of the upper Mississippi Valley amounting to 379,450,000 bushels, valued at $552,164,390. The chief value of these figures is to give some comprehension of the enormous economic importance to be attached to the rusts, and to justify from the purely commercial side the expenditure of time and money in their study.

Stem rust. — The most outstanding of the rusts of economic importance is the stem rust, *Puccinia graminis*. This species attacks wheat, oats, rye, barley, timothy, and a large number of wild and introduced grasses. It occurs in nearly all parts of the world, particularly in those regions well adapted to the growth of wheat, especially the exporting countries of Australia, South Africa, India, South America, and the hard red spring wheat region of the northern United States and western Canada.

Stem rust has its aecial stage on species of Berberis and Mahonia, chiefly on *B. vulgaris*. The uredinia and telia occur on the cereals mentioned above and on various other grasses. Sydow (1902–04) lists a world total of 176 species of telial hosts belonging in 39 genera. Arthur and Fromme (1920) list for North America 97 species in 34 genera.

The geneticist and cultivator must recognize many more forms than these, for there are physiologic races (p. 252) to be taken into account, which act more or less like independent species. Ten races of *Puccinia graminis* have been detected and named (Eriksson, 1894; Jaczewski, 1910; Stakman & Piemeisel, 1917), which are as follows:

P. graminis tritici on wheat, barley, rye, and grasses belonging to Hordeum, Agropyron, Elymus, Bromus, etc.

P. graminis avenae on oats, and certain wild grasses.

P. graminis secalis on rye, *Agropyron repens*, etc.

P. graminis agrostidis on species of Agrostis.

P. graminis poae on *Poa compressa*, *P. annua*, *P. pratensis*, and other species.

P. graminis phlei-pratensis on timothy, *Dactylis glomerata*, and species of Festuca.

P. graminis airae on *Aira caespitosa*.

P. graminis calamagrostidis on *Calamagrostis epigeios*.

P. graminis aperae on *Apera spica-venti*.

P. graminis arrhenatheri on *Arrhenatherum elatius*.

The first six of these are known to occur in America (Carleton, 1899; Freeman & Johnson, 1911; Stakman & Piemeisel, 1917; Stakman & Levine, 1922).

The physiologic races of *P. graminis*, besides differing in their action on different hosts, show slight differences in shape and size of the spores, and may be distinguished to a certain extent by biometric methods (Levine, 1923, 1928; Bailey, 1925).

Furthermore, each race is capable of being differentiated into physiologic forms (p. 255). Within one of the races, *P. graminis tritici*, 37 physiologic forms have been recognized in the United States (Stakman & Levine, 1922), and 24 in Canada, five of the latter being different from those reported from the United States (Newton, Johnson & Brown, 1928*a*, *b*). These forms are distinguished by their action on a selected list of differential hosts consisting of certain varieties and species of wheat. During a seven-year period 17 physiologic forms of the same race have been detected in western Canada, but only relatively few of these have been found in any one season (Newton & Johnson, 1927a). Similarly five different physiologic forms have been recognized in *P. graminis avenae* (Stakman, Levine & Bailey, 1923). There is evidence that there are similar forms in other races of *P. graminis*, particularly that of rye (Levine & Stakman, 1923).

Rust may be reduced to a certain extent by planting early maturing varieties, by seeding spring wheats as early as possible, and by avoiding poorly drained locations or the excessive use of nitrogenous fertilizers. Early harvesting (p. 72) has not proved advantageous (Harrington, 1928.)

FIG. 174. — Dusting a wheat field with sulphur by using an aeroplane. (After Bailey & Greaney, 1928.)

Spraying with fungicides was naturally one of the first direct control methods to be tried (Hitchcock & Carleton, 1893), but gave no promise of value, and the same negative results were shown in the case of stem rust of oats, and leaf rust of wheat, oats and barley (Kellerman, 1891; Pammel, 1892; Hitchcock & Carleton, 1893, 1894; Galloway, 1893). Recently dusting with sulphur has given promising results for several cereal rusts (Kightlinger, 1925; Bailey & Greaney, 1925, 1927; Kightlinger & Whetzel, 1926; Lambert & Stakman, 1926; Petri, 1926;

Greaney, 1928). In Manitoba various methods of application, including distribution by aid of the aeroplane (Fig. 174), have proved measurably successful against wheat rust (Craigie & Greaney, 1927; Bailey & Greaney, 1928).

The most practical and promising methods of control known at the present time appear to be the eradication of the alternate hosts and the selection and breeding of resistant varieties.

Although aecia are necessary to complete the life-cycle of stem rust, yet in some wheat-growing regions, notably southern Africa, Australia and the southern United States, the continuance and spread of the rust is not dependent on the barberry or mahonia, but is made possible through repeated propagation by the uredinia. In general it may be said that under conditions of mild winters stem rust can live throughout the year in the uredinial stage; either the spores remain viable from one season to the next, or late fall infections live over the winter season as mycelium which is capable of developing urediniospores the next spring.

In northern regions of Europe and North America, however, the barberry is necessary in many localities for the development of rust in a severe form and is sometimes primarily responsible for the continuance of the rust from season to season. Even in southern regions, especially when mountainous, the barberry is responsible for serious outbreaks of rust (Stakman, 1923; González, 1926).

The eradication of barberries to control rust was practiced to some extent even before the true relation of the barberry to wheat rust was understood (p. 42). In general it may be said that stem rust does not cause the wide-spread damage in Europe that it does in America, presumably because barberries have been more consistently removed from the grain growing districts. In Denmark a law was passed in 1903, and variously emended since, making the eradication of barberry compulsory. The result has been that serious outbreaks of stem rust no longer occur (Lind, 1915). Similar results have been obtained in Norway (Henning, 1916).

In the United States a campaign was begun in April, 1918, for the eradication of the various species and varieties of barberry, except the Japanese (*Berberis thunbergii*), from thirteen of the states in the upper Mississippi Valley: *viz.*, Colorado, Illinois, Indiana, Iowa, Michigan, Minnesota, Montana, Nebraska, North Dakota, Ohio, South Dakota, Wisconsin and Wyoming. From April, 1918, to June, 1927, about 7,000,000 barberry bushes and over 7,000,000 barberry seedlings

had been destroyed. The work was carried on with an outlay of $2,567,715 from federal funds, and $652,887 from state and other coöperative agencies, beside much assistance from private sources for which no estimate is available. The work of complete eradication has been hindered by the fact that barberries have spread from cultivation in many places and have become established in out-of-the-way places. The campaign is still in progress and the result cannot be predicted with certainty, as there are still many bushes to be eradicated. It may be said, however, that the loss from stem rust in the eradication area is much less, and that epidemics, particularly in the winter wheat sections, are local and usually traceable to the presence of barberry bushes. In the southern states, however, the problem of control is entirely apart from the eradication of the alternate host, and must be sought in cultural practices or the use of resistant varieties.

A large amount of attention has been given to selection and breeding of resistant varieties and considerable progress has been secured. This work is made difficult by the presence of physiologic forms, particularly in wheat rust (p. 255). A considerable number of varieties of wheat are now known, however, which are essentially immune to one or more physiologic forms. The results of breeding work indicate that varieties may be developed which are resistant to a considerable number of physiologic races or forms (Aamodt, 1923; Aamodt & Levine, 1925; Bailey, 1928; Barker & Hayes, 1924; Clark, 1925; Clark, Martin & Stakman, 1926; Comes, 1913; Dietz, 1925; Evans, 1911; Garber, 1922; Griffee, 1922; Harrington, 1925; Harrington & Aamodt, 1923; Hayes & Aamodt, 1923; Hayes, Stakman & Aamodt, 1925; Jaczewski, 1910; Jenkin & Sampson, 1921; Mackie & Allen, 1924; Mains, 1926a, b; Melchers & Parker, 1922a, b; Stakman, Levine & Griffee, 1925; Vavilov, 1913, 1914, 1919).

Wheat attacked by stem rust contains more crude protein and less carbohydrates in both straw and grain than wheat free from rust (Shutt, 1905; Snyder, 1905). Rusted wheat straw has a high feeding value, as it possesses "nearly twice as much protein as normal ripe straw, and as much as is present in prairie and timothy hay." It is readily eaten or even preferred by most farm animals (Snyder, 1905).

The stem rust of oats, *P. graminis avenae*, usually causes small losses, rarely reaching an epidemic stage. Breeding resistant varieties of good quality has met with some success. The variety "White Russian" ("White Tartar") has been found to be resistant to all physiologic forms of *P. graminis avenae* known in the United States, and hybrids with

spreading panicle and high quality have also been obtained that are equally resistant. However, there are physiologic forms in Canada, Sweden and South Africa to which "White Russian" and its hybrids are susceptible (Bailey, 1925; Gordon & Bailey, 1928), and these may eventually become common unless special precautions are taken to restrict them.

The stem rust of rye, *P. graminis secalis*, causes small damage in many countries. In Germany, however, where rye flour has been a staple food product for centuries, the economic loss from this rust is often very serious. In the "rust year" of 1891 the harvest of rye fell about 120 kilograms and wheat about 80 kilograms below the average for the previous ten years, creating a financial loss of about GM170,000,000 (Esmarch, 1926).

The stem rust of timothy (called herd's grass in some sections of North America), *P. graminis phlei-pratensis*, is often considered to be a distinct species under the name *Puccinia phlei-pratensis*. It does not readily pass to the various cereals, and infects the barberry only to a slight extent under exceptionally favorable circumstances. It was first observed in North America in 1886 at Madison, Wis., but is now common throughout the country (Kern, 1909). While injury to the host is undoubtedly considerable the rust does not assume epidemic form, and the amount of financial loss has never been estimated.

Stripe or yellow rust. — This rust, *P. glumarum*, attacks wheat, spelt, emmer, rye, barley and various grasses, and is widely distributed in Europe, Asia, and northern Africa. It does not occur in Australia or New Zealand. In North America it was first detected in 1915 (Humphrey, Hungerford & Johnson, 1924), and is now known along the Pacific Coast from British Columbia southward as far as Chile in South America (Arthur, 1925), and also through the Rocky Mountain region as far east as the Black Hills of South Dakota (Humphrey, Hungerford & Johnson, 1924). The losses from stripe rust in America are usually not large, except in Mexico where it is often abundant and highly injurious.

In England, northern Germany, and certain other sections of Europe, especially eastward, this rust has long been recognized and is considered the most serious of the several rusts attacking wheat in those parts. In addition to the growth upon the foliage and sheaths, stripe rust may occasionally develop on stems, glumes, awns, and even on the kernels in some very susceptible varieties. The potentiality for damage is therefore even greater than for the other rusts attacking the leaf.

In addition to the damage caused by the rust as a leaf parasite, the infection of glumes and kernels often results in still more shrunken grain of low quality and viability.

Five physiologic races of stripe rust have been recognized, *viz.: P. glumarum tritici* on wheat; *P. glumarum hordei* on barley; *P. glumarum secale* on rye; *P. glumarum elymi* on *Elymus arenarius*, and *P. glumarum agropyri* on *Agropyron repens* (Eriksson, 1894). In America only the first one has been detected with certainty, although there is evidence that the barley race is also present as well as another race on *Hordeum murinum* (Hungerford & Owens, 1923). No physiologic forms of the wheat race have been certainly distinguished, yet there is some evidence that they may occur.

The aecial stage for the stripe rust is unknown. It has been amply established that the rust is capable of overwintering in the uredinial stage practically throughout its range (Hungerford, 1923). It is claimed by some European investigators that stripe rust may be transmitted by infected kernels (Eriksson, 1897a; Massee, 1899; Beauverie, 1913; Blaringhem, 1914), but the opinion is generally discredited, and Hungerford (1923), who investigated this question most carefully, obtained no evidence in its support.

As with other cereal rusts, which are not dependent on the aecial stage to carry the fungus from one season to the next, the most practical method of control is in the selection or breeding of disease-resistant varieties. Fortunately there are a number of varieties of wheat now known which show marked resistance to the rust (Henning, 1919; Armstrong, 1922; Hungerford & Owens, 1923). Biffen (1922), a pioneer in the production of rust-resistant varieties of small grains, has demonstrated that "this rust can be controlled by the comparatively simple expedient of breeding." Judicious use of potash salts, however, has been found greatly to lessen the injury from stripe rust (Hicke, 1927).

Leaf or brown rust of wheat. — The leaf rust of wheat, *P. rubigo-vera tritici*, more often called *P. triticina*, is present in more or less severity in all regions where wheat is grown. Because of its wide distribution its importance in the wheat industry is second only to the stem rust. The loss in yield is due to a reduction in the number and size of the kernels (Fig. 175). In the United States in 1921 leaf rust is estimated to have caused a loss of over 23,000,000 bushels of wheat and in the five-year period from 1919–1923 inclusive an average annual loss of over 14,000,000 bushels. The extent of losses for other regions has not been available, but in 1890 the harm to Australian wheat was

"practically all" from the leaf rust (Cobb, 1890). In general it may be said, however, that losses from this disease have been greatly underestimated. In susceptible varieties the yield is sometimes reduced 50 per cent. The greatest losses in the United States are in the southern section where soft red winter wheat is grown, with lighter losses in the hard red winter wheat region centering in Kansas and in the hard red spring wheat region centering in North Dakota.

Greenhouse studies have shown that when susceptible varieties are heavily rusted during the whole period from the seedling stage to

A *B*

FIG. 175. — Comparison of heads from severely rusted and rust-free plants of Fulcaster wheat attacked by *Puccinia rubigo-vera tritici: A* an average normal head with the kernels from the four flowers of each spikelet arranged in a corresponding series, *B* an average head from a rusted plant showing fewer kernels, especially from the inner (*i.e.*, upper) flowers of each spikelet. (Photograph by E. B. Mains.)

maturity little or no seed is produced. When the rust is severe from the beginning of heading to maturity seed production is reduced 15 to 25 per cent, (Mains, 1927). This reduction appears to be due to the failure of the upper and lower spikelets in the head to produce seed, combined with the lessened number of seed produced in the middle spikelets (Fig. 175).

Leaf rust of wheat is one of a large group of grass rusts having aecia on ranunculaceous hosts, to which the collective name *Puccinia clematidis* or *P. elymi*, is often applied. It has been shown to have its aecia on species of Thalictrum (Jackson & Mains, 1921), especially certain eastern European and Asiatic species, notably *T. delavayi* and *T. flavum*. The distribution of these two hosts overlaps that of *Triticum vulgare* in west-central Asia, where wheat presumably originated and from which region the rust with its hosts has spread to all parts of the world.

The full rôle of the aecial stage for *P. rubigo-vera tritici* is unknown, as it has not yet been recognized with certainty from field collections. The aecial stage, however, is not essential to the propagation of the rust, as the species is able to overwinter in the uredinial stage. This apparently occurs throughout its range. On this account the leaf rust of wheat cannot be controlled to the same extent as stem rust by the eradication of its alternate host.

Leaf rust of wheat has been shown (Mains & Jackson, 1926) to consist of at least 12 physiologic forms distinguished by the manner in which they infect 11 selected differential strains of wheat (p. 255). It seems probable that a still larger number of such forms exists.

Studies of several crosses between different varieties of wheat in relation to inheritance of resistance to leaf rust give promise that strains of wheat may be developed by breeding in which resistance to the various physiologic forms may be combined (Mains, Leighty & Johnston, 1926; Mains, 1926b).

Leaf or crown rust of oats. — This rust, *P. coronata*, is the most common rust of oats, and although it is a leaf rust it is usually called "crown rust" because of the peculiarity of the teliospores, which have stout projections from the wall of the upper cell (Fig. 176) suggesting a crown. It is world wide in distribution, occurring in more or less severe form wherever oats are grown. For some seasons in certain sections of the country it is the limiting factor in successful oat culture. Annual losses in the United States for the five-year period of 1919–1923 inclusive averaged over 15,500,000 bushels. Losses for the state of Iowa alone for this period averaged over 2,000,000 bushels.

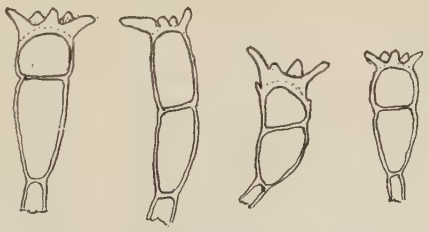


Fig. 176. — Four teliospores of *Puccinia coronata*. (After Bolley, 1889b.)

The aecia of crown rust occur on various species of Rhamnus and the telia not only on oats (*Avena sativa*) but on many species of grasses belonging to a number of genera, among which Calamagrostis, Lolium, Holcus, Dactylis and Festuca are prominent. There are 39 species in 21 genera listed in the North American Flora as hosts for this species (Arthur & Fromme, 1920).

The rôles of different aecial host-species in connection with physiologic specialization have been extensively studied both in Europe and America. In general it may be said that the investigations so far made indicate that the species does not show the sharp host specialization or separation into races which is shown by *P. graminis*. All of the races studied in America develop on *Avena sativa*. Aecia for the most common race on oats develop on a number of species of Rhamnus. In Europe the

Fig. 177. — Field of oats in Iowa near a hedge of *Rhamnus cathartica:* the plants barely knee high, and so rusted that the yield did not pay expense of harvesting. (After Dietz, 1923.)

most important aecial host is *R. cathartica*. In America the introduced *R. cathartica* (p. 166) and to some extent the native *R. lanceolata* are important (Melhus & Durrell, 1919; Melhus, Dietz & Willey, 1922; Dietz, 1926b). A ten-acre field of oats at Clarion, northern Iowa, with a hedge of *R. cathartica* along one side showed, according to Dietz (1923), an infection of crown rust in 1921 amounting to 100 per cent adjoining the hedge and fading away to a small amount at the opposite side of the field. Near the hedge the plants were scarcely knee high (Fig. 177), and the yield of grain did not warrant harvesting. The comparison in growth of plants from opposite sides of the field was very marked

(Fig. 178). The native species of Rhamnus are rarely planted either for hedges or ornament, and only exceptionally are responsible for epidemics. Studies with urediniospores have shown the existence of physiologic forms in *P. coronata avenae* (Hoerner, 1919; Parson, 1927).

As with other cereal diseases due to rusts spraying was at first tried as a control (Kellerman, 1891), but the most practical method at present seems to lie in the development of varieties which are resistant (Parker, 1918; Vavilov, 1919; Durrell & Parker, 1920).

LEAF RUST OF RYE. — The leaf rust of rye, *P. rubigo-vera secalis*, often treated under the names of *P. dispersa* and *P. secalis*, is nearly coëxtensive with the distribution of the host. It is especially abundant throughout Europe and North America. It has not been reported from Australia or South America.

FIG. 178. — Two samples of oats taken on July 1 from the field shown in Fig. 177: *A* near the hedge of Rhamnus, with 100 per cent of crown rust, *B* from opposite side of field, with practically no rust. (After Dietz, 1923.)

In economic importance this rust is quite similar to the leaf rust of wheat, when the relative value of the two hosts is considered, remembering that in parts of Germany and eastward the rye crop predominates. Losses in the United States for the seven-year period of 1919–1925 inclusive averaged 163,000 bushels, the loss for the year 1919 being estimated at 538,000 bushels.

The aecia of this rust occur on *Anchusa officinalis* and *A. arvensis* in Europe. De Bary who first established the connection (p. 54) states that aecia were found throughout the season from spring till fall (1866a). The aecia have not been found in nature in America except on the cultivated *Anchusa capensis*. Culture work, however, has established the fact that the rust in America will infect *Anchusa officinalis*. The teliospores are mature and may germinate in the fall or they may overwinter and germinate in the spring (Mains & Jackson, 1924).

The aecia are apparently not essential to the propagation of the rust, even in Europe, as it has been shown by a number of investigators that the rust is capable of overwintering in the uredinial stage. Two physiologic forms have been shown to exist (Mains, 1926b).

Resistant individuals have been found in a number of varieties of rye. A study of the inheritance of resistance in crosses made between resistant individuals indicates that resistance is probably dominant (Mains & Leighty, 1923). Rye, however, unlike wheat, is cross pollinated and in general is self sterile, which makes it difficult to develop resistant varieties. A strain of the variety "Abruzzes" has been studied by Mains (1926a) which is fairly self fertile and from it resistant lines have been isolated which are apparently homozygous for resistance to leaf rust.

Leaf rust of barley. — The leaf rust of barley, *P. anomala*, is in general of minor importance, but when it occurs in severe form is capable of losses comparable to those of other leaf rusts. This rust is quite generally distributed in the northern hemisphere and also occurs in Australia. It is found only on cultivated barley.

The aecial stage occurs on species of Ornithogalum, as was first demonstrated in Russia (Tranzschel, 1914) and afterward confirmed in America (Mains & Jackson, 1924), Austria (Beck, 1924) and France (Ducomet, 1926). The rôle which this aecium bears to the overwintering of the rust is not known. It seems probable that throughout most of its range *P. anomala* is not dependent on the aecial host for its maintenance, but may overwinter in the uredinial stage.

No detailed study of specialization or varietal resistance in this species has been published. It has been shown, however, that at least two physiologic forms exist, as indicated by their difference in reaction on three selected varieties of barley (Mains, 1926b).

Corn rust. — Corn rust or leaf rust of corn (maize), *P. sorghi*, is an American rust which has spread along with its host to all parts of the world where corn is grown. It occurs on all types of corn with varying degrees of severity. While in general a minor disease of this crop, a loss of over 3,000,000 bushels was recorded for Iowa in 1925. In the United States it appears to be most serious as a rule in the southern states, particularly those bordering the Gulf of Mexico. As a disease of sweet corn, rust often does considerable damage. Weber (1922) lists the types of corn in descending order of susceptibility as follows: sweet, flint, flour, dent, pod, and pop. In addition to *Zea mays* this rust occurs on *Euchlaena mexicana* and possibly also on *Andropogon furcatus*.

The aecia are produced on species of Oxalis, of which the most important one is *Oxalis stricta*. While it is possible that this rust may overwinter in the uredinial stage the fact has not been established. Aecia may be much more common than the records indicate. It has been shown that highly resistant individuals occur in nearly all groups of corn (Mains, Trost & Smith, 1924), and that selfed lines may show either high resistance or susceptibility. Physiologic forms occur in this species and a number have been isolated (Mains, 1926b; Stakman, Christensen & Brewbaker, 1928), which can be distinguished by their action on selected lines and varieties of corn (p. 255).

Sorghum rust. — A leaf rust, *P. purpurea*, occurs on sorghum, *Holcus sorghum*, Johnson grass, *H. halepensis*, Sudan grass, *H. sorghum sudanensis*, and closely related varieties and species throughout the subtropical regions of both hemispheres. The rust causes bright purplish spots on the leaves, often in great abundance. In some regions, particularly in India (Butler, 1918b), it is reported as causing considerable damage.

The aecial stage is unknown. No special study looking toward the development of resistant varieties has been reported, but it seems reasonable to expect that resistant varieties could be found by modern breeding methods, should the necessity arise.

THE RUSTS OF FRUIT TREES

The rusts attacking fruit trees belong in large part to the genus Gymnosporangium, which is unique in that the aecial stage for all but three of the forty-three or more known species occur on Malaceae and the telia on Cupressineae. Due to the absence of repeating spores all of the diseases of cultivated fruits caused by members of the genus can be eliminated by the removal of the telial host. Repeating spores are known in only one species, and this species has recently been made the basis for an independent genus, Gymnotelium (p. 113).

A few species of rusts belonging to other genera attack fruit trees, but with one exception, *Tranzschelia punctata* (p. 344), are not of sufficient economic importance to require mention here.

Apple rust in eastern United States. — The apple rust of the eastern United States, *Gymnosporangium juniperi-virginianae*, is a disease of that region second only in importance to apple scab or fire blight. This rust occurs throughout the range of the telial host, *Juniperus virginiana*, which includes the greater part of the area east of the Rocky Mountains. It is most severe as a disease of the cultivated apple in

the prairie regions of the central Mississippi Valley and in some of the interior valleys of Virginia and West Virginia (Pammel, 1905; Stone, 1908; Heald, 1909; Jones & Bartholomew, 1915; Schneiderhan, 1926). The losses in the apple crop are often large. In 1912 in one county in West Virginia the loss was estimated at $75,000 and for a similar area in Virginia in 1917 at $100,000. The loss for the entire Virginian region in 1920 was 3,217,000 bushels and in 1922 was 4,129,000 bushels.

The aecial stage of the rust occurs only on species of Malus and the telial stage only on *Juniperus virginiana* and the closely related *J. barbadensis*. Pycnia and aecia are mature in midsummer when the aeciospores are carried by the wind to the cedar and, if in germinable condition (p. 374), infection occurs. There is no visible effect until the next season in early summer. Galls then begin to appear, which develop to full size during the growing season but do not produce telia till the following spring. The teliospores germinate at once and the basidiospores are carried to the apple and cause infection. It thus takes two full years for the life-cycle to be completed, although teliospores are in condition to cause infection immediately upon maturity (Heald, 1909; Stewart, 1915; Weimer, 1917b).

On the apple the leaves, fruits, and occasionally the twigs, are attacked. The greatest damage results from leaf infections which, when numerous, cause premature defoliation and in any case retard photosynthesis and increase transpiration. The effect of a serious foliage infection results not only in a reduction in the number of fruits which set, but also in their size. The general effect on the trees is severe. Vitality is lowered, few fruit buds are formed and the tree enters the winter in a weakened condition. A severe foliage infection may mean the loss of the greater part of two crops.

When infection occurs on the fruit the loss is a direct one. The lesions develop more commonly on the calyx end but may occur at any point on the fruit. Usually pycnia are formed and frequently mature aecia, but occasionally only an obscure spotting results, especially on resistant varieties. The general effect is to cause malformed and worthless fruits or, when less severe, to increase the percentage of culls (Reed & Crabill, 1915; Giddings & Berg, 1915b; Fromme, 1919).

On the cedar the rust causes the development of brownish galls which when mature may reach a diameter of two inches (Fig. 164). These develop from the bases of leaves. When mature the galls show small circular depressions scattered over the surface, from which telia develop the following spring. The telia are long gelatinous horn-like projections,

and when fully expanded may reach a length of one inch (Fig. 179). These telial columns are made up of the expanded gelatinous bases of the teliospores which absorb water during spring rains.

Fig. 179. — Gall of the "cedar apple," *Gymnosporangium juniperi-virginianae*, with the telia fully expanded. (After Kern, 1911.)

From the fact that in the life history of this rust there are no summer or repeating spores, the rust cannot be maintained on either host in the absence of the other host. The most practical method of control is the removal of cedars from the vicinity of orchards. While it has been shown that infection may sometimes occur over a range of six to eight miles, in practice it is found that if cedar trees are removed within a radius of one or two miles from the orchards, the disease can be satisfactorily controlled. There have been extensive spraying tests carried out with good results, when they have been conducted by skilled pathologists and the applications properly timed with reference to teliospore germination. Spraying is not recommended, however, as a general orchard practice (Heald, 1909; Giddings & Berg, 1916; Fromme & Thomas, 1917; Fromme, 1919).

In Virginia and West Virginia special legislation relative to the cedar has been enacted, and large areas in orchard districts have been freed of cedar trees. A recent law[1] in Virginia requires the removal of cedar trees within two miles of an apple orchard.

Varieties differ in their relative susceptibility to rust and a knowledge of this fact is of value in planning to establish a new orchard (Giddings & Berg, 1915b).

Another American rust, *G. globosum*, forming its telia on the same species of cedar as the preceding, but having aecia chiefly on Crataegus, sometimes attacks the leaves of the apple in the eastern United States.

[1] The constitutionality of the law has been upheld. United States Supreme Court Reports, Law Edition **72**: 250–252.

On the cedar it produces globoid galls somewhat resembling those of *G. juniperi-virginianae*, but smaller.

Apple rust in Japan and China. — An apple rust, *G. yamadae*, occurs in Japan and China which has an equal capacity for producing injury to the cultivated apple as the similar American species, *G. juniperi-virginianae*. The two species have much the same general appearance and habit.

The rust attacks foliage, small branches, and fruit, even causing the death of twigs (Fukushi, 1925). It occurs not only on the cultivated apple, but also on several other species of the genus Malus, including *M. toringo*, *M. spectabilis* and *M. baccata*. The apple varieties "McIntosh Red" and "Fameuse" are relatively resistant. The telial stage occurs on the branches of *Juniperus chinensis*, producing small globoid galls.

Pear and quince rusts in United States. — In the Rocky Mountain region a common rust of the western mountains, *G. nelsoni*, with the telial stage on several species of cedar, and the aecial stage commonly on Amelanchier, has proved at times to do considerable damage. It attacks the fruits of pear and quince with unusual vigor.

In the eastern United States a species of Gymnosporangium, native to North America and common throughout the larger part of the continent, *G. germinale* (*G. clavipes*), sometimes attains considerable economic importance by its attack on the quince (Halsted, 1893; Sturgis, 1895; Stone & Smith, 1898; Stewart, 1910). Its most usual hosts are various species of Crataegus, Aronia and Amelanchier. Occasionally it spreads to the apple, affecting both fruit and twigs. The telial stage occurs on different species of Juniperus. This species of rust is notable for a wider range both of aecial and telial hosts than any other in the genus. Because of its omnivorous tendency and aggressive character it is likely to come into economic prominence whenever conditions are favorable.

A rust, *Gymnotelium blasdaleanum* (*Gymnosporangium blasdaleanum*), occurs in western Oregon and northern California. The disease has been noted as most serious on pear and quince, occurring occasionally on the apple as well as other cultivated and native species of Malaceae. In the near vicinity of the telial host this rust may assume considerable importance. The telial stage of the rust occurs only on the incense cedar, *Libocedrus decurrens*. The most common aecial hosts are the native *Crataegus douglasii*, *Amelanchier alnifolia* and *Malus rivularis*. Aecia also occur on the pear and quince, more rarely on the apple, and

occasionally on species of Sorbus, flowering crabs and Japanese quince that are cultivated for ornament. It attacks the fruits, leaves and smaller branches.

One of the features of this disease is the malformations caused by the aecial stage, especially on the fruit. Pears are usually attacked when young and are considerably distorted. If the infection occurs only on one side, the fruits are bent toward that side. Considerable hypertrophy may result when infection takes place on the blossom. Malformations of the quince fruits are particularly common and conspicuous, and the branches may be variously bent and twisted.

The telia occur on the leaves of the cedar as small brown pulvinate sori. No galls are formed but the rust occasionally becomes systemic in the branches, and large and conspicuous witches' brooms are formed. There are no uredinia.

No experiments for control have been conducted. It has been noted, however, that pear trees sprayed with lime sulphur for scab just before blossoming were less seriously affected than unsprayed trees. The disease, like others of its kind, can be eliminated by removal of its only alternate host, the incense cedar. The cedar is, however, a valuable forest tree, and is occasionally planted for ornament. Its presence near orchards must be considered a menace (Jackson, 1914, 1915).

Pear and quince rusts in Europe. — The most common and serious disease in Europe due to a species of Gymnosporangium is the pear rust, *G. sabinae*. This rust occurs throughout Europe. The aecial stage is found most commonly on *Pyrus communis*, though other species of Pyrus are often attacked. It does not occur on the quince or apple. The most common telial host is *Juniperus sabina*.

The rust attacks leaves, young twigs and fruits. Tubeuf (1907) presents evidence that the rust occasionally may be perennial in the branches of the pear, but Trotter (1916) does not consider this to be probable in Italy. While spraying has been recommended as a control measure, the removal of the telial host is considered more practical.

A rust much like the preceding, and for a long time confused with it, *G. mespili* (*G. confusum*), is common in Europe and central Asia. It has the same telial host as *G. sabinae*, but has as its aecial hosts various species of Crataegus, and especially the quince (*Cydonia vulgaris*) and medlar (*Mespilus germanica*), but does not attack the apple and rarely the pear. Another species of Gymnosporangium common in both Europe and North America, *G. clavariaeforme*, often proves harmful to pears in Europe, but only rarely so in North America. It produces

fusiform swellings of the branches of *Juniperus communis* and *J. sibirica* (*J. nana*). Its most usual aecial hosts are species of Amelanchier and Crataegus.

Pear and quince rusts in the Orient. — A rust common in eastern Asia on various species of Pyrus and Cydonia, *G. koreaense* (*G. asiaticum*), is capable of causing appreciable injury. The telial stage occurs on *Juniperus chinensis*. This rust made a sporadic appearance some years ago, both on the eastern and western coasts of the United States (Clinton, 1913; Jackson, 1916), having spread from cedars imported from Japan. Its early discovery, however, will probably lead to complete extermination from the western hemisphere.

A rust, *G. shiraianum*, very similar to the preceding, has proved even more destructive to pear culture along the coastal areas of central Japan (Tanaka, 1922). The telia occur on *Juniperus conferta* (*J. litoralis*). It has caused the growing of pears to be abandoned in some districts.

Rust of stone fruits. — A rust of considerable economic importance, *Tranzschelia punctata* (*Puccinia pruni-spinosae*) occurs on nearly all of the stone fruits, including peach, prune, cherry, nectarine, apricot, and almond. This rust occurs throughout the world wherever these crops are cultivated. It is primarily a foliage disease and in cases of severe infection may cause complete premature defoliation of the trees. It may also attack the fruit and young twigs, the latter especially among nursery stock. On the twigs cankers are produced in which uredinia live from one year to the next and perpetuate the rust.

The rust is heteroecious. The aecia (*Aecidium punctatum*) occur on species of Anemone, Hepatica and Thalictrum and the uredinia and telia on a considerable number of species of Prunus, Amygdalus and related genera. The aecia are not always required for the propagation of the species, particularly in the warmer regions of its range, where the rust occurs in greatest severity, largely in the uredinial stage.

Spraying has been recommended as a control measure in California, Oregon, Australia and New Zealand (Pierce, 1894; Cunningham, 1925; Goldsworthy, 1928). Plowing under the fallen leaves will also assist (Cunningham, 1925). The eradication of aecial hosts in the vicinity has also been suggested (Brooks, 1911), which will doubtless prove most serviceable in northern regions where the climate does not permit overwintering of the urediniospores.

Rust of figs. — A rust of figs, *Cerotelium fici* (*Uredo fici*), is common on the leaves of various species of Ficus throughout tropical and subtropical regions of both hemispheres. It covers the under surface of

the leaves with salmon-colored, powdery pustules of the uredinial stage, resulting in gradual defoliation. The full life-cycle of the fungus is unknown. The telia have been seen only in India on *Ficus glomerata*, an evergreen shade tree of Burma and India (Butler, 1914).

The rust usually appears so late in the season that it does not often affect the size of the fruit, but the defoliation resulting exposes the fruit to sunburn. It must also reduce the vitality of the trees, yet such is the vigor of recovery that no injury is apparent.

Destroying the fallen leaves by burning or burying, and spraying early in the season, have been suggested as means for control (Edgerton, 1911; Matz, 1918). Spraying with Bordeaux mixture as soon as the rust appears, and afterward as often as needed to protect the new growth, has been found to insure normal development and to prevent premature falling of the leaves (Lanham, Wyche & Stansel, 1927).

Rust of coffee. — A rust of coffee, *Hemileia vastatrix*, generally known as the "coffee-leaf disease," first attracted attention in 1868 as an epidemic in Ceylon and has now spread to all coffee growing regions of the Old World (p. 173). It attacks the leaves, causing a rapid and early defoliation. The full life-cycle of the rust is unknown. Although telia are occasionally met with, yet the uredinia are responsible for most of the injury and for the spread of the disease from tree to tree. It has greatly restricted the production of coffee in India, Java, the Philippines and intermediate sections. The exports of coffee from Ceylon decreased from about $15,000,000 in 1880 to $125,000 in 1909, due almost exclusively to the rust.

Much attention has been given to methods for controlling the disease. Those found to be most successful are removal of old trees and spraying the others with Bordeaux mixture, selection of more resistant varieties of coffee, destruction of fallen leaves, and choosing a relatively cool and dry location for the plantation.

THE RUSTS OF SMALL FRUITS

Orange rust of raspberries and blackberries. — The well-known disease of blackberries, dewberries, and black raspberries, commonly referred to as orange rust, *Gymnoconia interstitialis*, is especially abundant in the eastern United States and Canada and less common in other sections of North America and in northern Europe. The rust occurs on both wild and cultivated species and when abundant on the latter is of very considerable economic importance.

The rust is autoecious, and in its aecial stage is systemic and perennial

(p. 312). The infected shoots are depauperate, much drawn and usually sterile. The sori overspread the under side of the leaves and give the bright orange-red color characteristic of the rust. The telial stage is less abundant and causes no distortion of the leaves and no appreciable injury to the host. The sori are light-brown and inconspicuous. There are no uredinia (Clinton, 1893; Tranzschel, 1893).

Infection usually takes place in the young buds formed when the tips of stems take root. From the buds the mycelium spreads into the roots and crown, and the canes arising from such buds show systemic infection year after year. Infection may also enter the nascent buds upon the older canes, and in such cases only the growth from these buds will develop the rust (Dodge, 1923c).

As the rust is perennial in its aecial stage, the only practical method of control is to eradicate completely the affected plants as soon as they can be detected in the spring and before the aecia are fully developed (Dodge & Wilcox, 1926).

A microcyclic form of this rust, *Kunkelia nitens*, which resembles the aecial stage of the preceding in all outward appearances and in habit, is especially abundant in northeastern United States and adjacent Canada (Arthur, 1917b; Dodge, 1923d). It causes the same degree of injury as the macrocyclic form, and the same method of control is required.

Yellow rust of raspberries. — Another disease, *Phragmidium imitans*, confined to red and black raspberries, is widely distributed in the northern United States and Canada. This rust attacks the foliage and occasionally the fruits and stems, especially in the northwestern United States. When abundant it may cause serious defoliation and injury to the fruit. The "Cuthbert" and "Antwerp" varieties are reported as particularly susceptible. No remedial measures have been suggested except to encourage clean cultivation and such other cultural practices as make for a high degree of field sanitation (Dodge & Wilcox, 1926; Zeller, 1927).

A rust, *Phragmidium rubi-idaei*, on the red raspberry of Europe, very similar to the one just mentioned, and possibly to be considered a form of the same species, possesses similar capabilities of damage. It is a leaf rust that hastens the maturity of the foliage. It is suggested that spraying with potassium sulphide or Bordeaux mixture will serve as a control (Grove, 1913b).

Late raspberry rust. — A rust disease, now commonly referred to as the late raspberry rust, *Pucciniastrum americanum*, which is some-

times confused by growers with the orange rust or the yellow rust, is known to occur on a number of species of wild red raspberries and is reported occasionally as causing damage in cultivated red and purple varieties. It is most common in the northeastern United States and adjacent Canada.

This rust attacks the foliage and when in epidemic form causes serious defoliation of the plants late in the season. The fruit also may be attacked, and the canes as well. The species is undoubtedly heteroecious, the aecial stage probably occurring on the leaves of Abies or Tsuga. The connection, however, has not yet been demonstrated.

Cane rust of blackberries. — A rust of blackberries, *Kuehneola uredinis*, which occurs commonly on native species in the eastern United States as well as in Europe, often attacks the cultivated varieties of blackberries and dewberries. The most serious effect of this rust is the damage to the fruiting canes. The bark of badly infected canes splits open, exposing the golden- or lemon-yellow mass of urediniospores. Such canes dry out to such a degree that proper ripening of the fruit is prevented. The rust also occurs on the foliage, where the infection may be so severe as to injure the next season's fruit crop.

This rust is an autoecious species. The aecia commonly appear on the overwintered canes and foliage early in the spring, infection evidently having occurred in the fall. The uredinia and telia appear on the leaves, the latter being colorless.

It is recommended to burn badly infected canes and to practise clean cultivation (Dodge & Wilcox, 1926).

Currant and gooseberry rust. — Cultivated varieties of currant and gooseberry are occasionally attacked by the aecial stage of *Puccinia grossulariae*, the uredinia and telia of which occur on various species of Carex. The most frequent mention of trouble from this rust is in European literature. Both foliage and fruit may be attacked, though it is only rarely that the rust occurs in sufficient amount to be of serious account. This rust should not be troublesome where clean cultivation is practiced or where sedges of the genus Carex are eliminated in the vicinity of cultivated gooseberries and currants, since the infection of the latter develops only from the teliospores borne on the Carex.

Grape rust. — A rust of the grape-vine, *Phakopsora vialae*, usually cited under the name *Uredo vitis*, is common in subtropical regions, especially on *Vitis vinifera*. It occurs from Florida to Cuba, Jamaica, Porto Rico and Trinidad, and on *Vitis inconstans* and *V. flexuosa* in Japan, and on *Vitis lanata* in Java. It also occurs in Central and

South America. The telial stage is rare, reported only from Japan and Florida.

This rust attacks the leaves and may cause serious injury due to defoliation. There is evidence that certain varieties are more or less resistant (Shear, 1924). No remedial measures have been worked out.

THE RUSTS OF VEGETABLE CROPS

Asparagus rust. — The rust of asparagus, *Puccinia asparagi*, offers an excellent example of a rust disease for which control measures have been developed, that appear to be entirely adequate. This rust was long known in Europe but was not regarded as a serious disease. It was introduced into America sometime previous to 1896, and quickly spread through the eastern United States and later reached the Pacific Coast (p. 175). The damage caused by this disease during the early years of its spread in this country was so great that in some sections a very profitable industry was almost wiped out. Its seriousness and importance may be judged by the considerable number of special bulletins which were published by the State Experiment Stations between 1898 and 1906 (Halsted, 1898a; Anderson, 1899; Stone & Smith, 1899; Pammel & Hodson, 1900; Sirrine, 1900; Arthur, 1901; Smith, 1905, 1906). With the exception of certain cereal rusts, the eastern apple rust and the blister rust of pines, no plant disease caused by this group of parasites has received as much study in the United States with such satisfying practical results as the asparagus rust.

When severely attacked the tops of the plants dry up prematurely, and a repetition through several seasons so weakens the roots and crowns that few edible stalks are produced.

The rust is autoecious. Aecia are commonly formed on the young shoots in the spring. In commercial plantings most of the aecial stage is eliminated in cutting for market, so that the rust usually spreads from adjacent wild plants and young plantations. The chief injury is from the uredinial stage, which is capable of spreading and multiplying with great rapidity.

In the early development of this disease spraying with Bordeaux mixture was tried with indifferent success. When resin-fish-oil sticker was used with the Bordeaux favorable results were obtained, but the expense of the frequent sprayings that were required and the fact that only partial control was obtained, prevented this method from coming into general use. In California excellent results have been obtained with three applications of sulphur dust (Smith, 1905, 1906).

At the time when the rust first appeared in severe form "Connover's Colossal" was the most popular variety, particularly for canning. It was soon found that this variety was extremely susceptible to the rust, and was soon replaced by strains of "Palmetto," which proved more resistant. The latter group of varieties, however, was not suitable for canning because of coarseness and color. On this account a thorough study of resistance was begun which culminated in the introduction of varieties suitable for various purposes and resistant to the rust. The most important of these are the Washington varieties developed and introduced by Norton (1913, 1919).

Bean rusts. — The beans, commonly known in America as field, garden or pole beans and in Europe as kidney, French or haricot beans (*Phaseolus vulgaris*) are subject to a rust, *Uromyces appendiculatus phaseoli*, in nearly all parts of the world, which in central Europe and eastern United States is of considerable economic importance. The rust attacks the foliage primarily and may be so severe as to cause complete defoliation and great reduction in yield. The rust also may injure the pods and stems.

It is an autoecious species, but the aecial stage is rarely seen in the field, yet is easily demonstrated by cultural methods. The damage is caused primarily by the abundant development of the uredinial stage.

Varietal susceptibility has been extensively studied (Gassner, 1909; Jordi, 1916; Fromme & Wingard, 1918, 1921), and marked differences have been shown to exist among standard varieties, some being practically immune, but no definite evidence of the presence of physiologic races has yet been observed.

The beans commonly known in Europe as field or broad beans and in America as English or horse beans (*Vicia faba*) are subject to an entirely different rust, *Uromyces fabæ*, which also occurs on the field vetch (*Vicia sativa*) and other species of Vicia and on Lathyrus, both wild and cultivated, and also on the pea (*Pisum sativum*). It is to be found in every part of the world. Like the other bean rust it is autoecious and chiefly harmful in the uredinial stage. The aecia are rarely observed, and only in northern regions, while the telia are equally absent in tropical regions. A promising suggestion regarding control measures in northern regions is to destroy the teliospores by burning the refuse of the crops (Grove, 1913b).

Pea rusts. — Besides the autoecious rust of peas already mentioned (*Uromyces fabae*), a heteroecious rust, *Uromyces pisi*, exists in Europe, which has not been found in America, although erroneously so reported.

The aecial stage produces a perennial mycelium and becomes systemic in species of Tithymalus (Euphorbia). The continued existence of the rust, however, is not dependent upon the alternate host.

Neither this rust of the pea nor the preceding one becomes of economic importance except occasionally under favorable circumstances.

Beet and spinage rusts. — The garden varieties of beets, as well as sugar beets and mangels, are subject to a rust known as *Uromyces betae*. The rust is widespread in Europe, and occurs in southern Africa, New Zealand and Australia, but in America has appeared only in southern California. It is an autoecious species, but is propagated and causes injury chiefly in the uredinial stage.

An American heteroecious rust, *Puccinia subnitens*, occurring abundantly in both North and South America on salt grass (*Distichlis spicata*) has appeared in its aecial stage on spinage in the vicinity of Walla Walla, Washington, and adjacent Oregon, doing considerable injury (Barss, 1922). The same kind of injury has also occurred to beets in Colorado (Pool & McKay, 1914), and is also reported from Utah. As the injury can only occur in the vicinity of rusted salt grass, the easiest way to avoid it is either to destroy the near-by salt grass or remove the spinage and beet fields to a distance.

Peanut rust. — A rust, *Puccinia arachidis*, occurs on the ground nut, goober, or peanut in various sections of South America and quite generally throughout the West Indies. It appears only as uredinia and is often destructive, especially in the West Indies. Telia have been reported only once, from Paraguay.

When the rust appears toward the end of the season it does little damage, but with an early attack, especially on wet soil, considerable defoliation, premature ripening of the halms, and a large proportion of shriveled kernels, may result. It is more prevalent in wet seasons. Spraying with Bordeaux mixture has in some cases proved beneficial (South, 1911; Robson, 1916; Nowell, 1915, 1923).

THE RUSTS OF FORAGE CROPS

Clover rusts. — Various kinds of clovers, both wild and cultivated, are attacked on leaves and stems by *Uromyces trifolii*. The rust is distributed throughout both hemispheres, but is rare in the warmer regions. There are a number of physiologic races, some of which are usually treated as distinct species (Liro, 1906; Kobel, 1920; Davis, 1924; Mains, 1926b).

The rust on *Trifolium pratense*, or red clover, *U. trifolii fallens*, and

the one on *T. hybridum*, or alsike clover, *U. trifolii hybridi*, probably cause the greatest injury, and especially so in the latter part of cool and moist seasons. The aecia of these rusts are rarely seen, the uredinial stage being the most prominent and injurious. The rust on *Trifolium repens*, or white clover, *U. trifolii trifolii-repentis*, is usually abundant, producing aecia freely in the early part of the season, but is generally not noticeably injurious.

Other races doubtless occur, but have not been carefully studied. Studies by Mains (1926b) show that a high degree of resistance exists in individual plants both of the white and red clovers, which holds out the promise of valuable results when suitable breeding experiments are undertaken to secure rust-proof varieties.

Another rust, *Uromyces flectens*, occurring locally on white clover in North and South America and in Europe is without economic importance. It forms no uredinia.

Alfalfa rust. — A foliage rust of alfalfa, *Uromyces striatus* (*U. medicaginis*), is common in North America and Europe, and has been reported from various other sections of the world including Australia and South America. While usually not of much economic importance, yet when conditions are favorable it is capable of causing seriously premature ripening and hence loss of the forage.

The species is heteroecious, having its aecia on several species of Tithymalus. The aecial stage has not been seen outside of central Europe. The rust is able to maintain itself by means of the uredinia. In addition to alfalfa a number of other species of Medicago are hosts for this rust. Mains (1926b) has shown that individual strains of alfalfa can be found which are highly resistant.

Cowpea rust. — A rust of the cowpea, black pea, or China bean, as it is variously known, and of related plants, *Uromyces appendiculatus vignae*, which has commonly been confused with the bean rust, is of cosmopolitan occurrence wherever the chief host, *Vigna sinensis*, is cultivated. The rust is autoecious and has a capacity for damage similar to that possessed by the bean rust. In addition to the cowpea this rust is recorded on *V. repens*, *V. sesquipedalis*, *V. vexillata*, *Dolichos lablab* and *Phaseolus truxillensis*.

A study of varietal susceptibility (Piper, 1912; Peiterson, 1923; Fromme, 1924) has shown most fortunately that the larger number of the varieties studied are immune or only slightly susceptible.

Sunflower rust. — This rust, *Puccinia helianthi*, while common on cultivated and wild sunflowers in America, Europe and Australia, was

considered of little economic importance until the plant came to be grown extensively as a silage crop. Under these conditions the rust has assumed considerable prominence because of its tendency to cause premature ripening of the leaves, and even defoliation.

Spraying and dusting with copper compounds have proved ineffective. Three races or strains of the rust have been distinguished by their action on different species of Helianthus (Bailey, 1923). Selection of resistant varieties appears to be the most promising method of control. "Kaeurpher," a South American variety, has been reported from Michigan as resistant (Spragg & Down, 1920).

THE RUSTS OF ORNAMENTAL PLANTS

Snapdragon rust. — A destructive rust of the garden snapdragon, *Puccinia antirrhini*, first recorded from the vicinity of San Francisco, California, in 1895 (Blasdale, 1903), has now spread throughout the United States and Canada and to Bermuda, both in gardens and greenhouses (p. 172). This rust is very destructive, frequently resulting in the death of plants in the garden and complete loss of the crop in the greenhouse.

Only urediniospores and teliospores are at present known. Since it has been shown (Hockey, 1921; Mains, 1924b) that the basidiospores can not reinfect the snapdragon it is probable that the rust is heteroecious. It is known to occur in California on native species of Antirrhinum. The rust presumably maintains itself from season to season by means of the uredinial stage, which is the one most abundant in greenhouses.

Because of its importance as a disease of a florist's crop this rust has received considerable study, especially with reference to the conditions favorable for its development and of means for its control (Peltier, 1919; Doran, 1921; Butler, 1919, 1923; Mains, 1924b).

In greenhouse culture, particularly when plants are grown from seed, little trouble from this disease is now experienced when proper sanitation and cultural methods are practised. Dusting with sulphur is effective if high temperatures are maintained. In field and garden culture the problem of control is more difficult, and in northern sections dusting with sulphur has not proved consistently reliable. In warmer regions, however, this method may be of value. Some attention has been given to the study of resistant varieties (Doran, 1921; Mains, 1926b), and breeding for rust resistance gives promise of leading to effective results both in greenhouse and garden culture.

Carnation rust. — The rust of carnations, *Uromyces caryophyllinus*, is a native of southern Europe where it has been known for many years. It was introduced into England about 1890 and into America sometime previous to 1891 (p. 172), and soon attracted much attention because of the severe losses which it caused in greenhouses. It quickly spread throughout North America and around the world wherever the carnation is grown as a greenhouse crop, largely by the distribution of diseased cuttings. For a time the rust threatened to be a serious handicap to

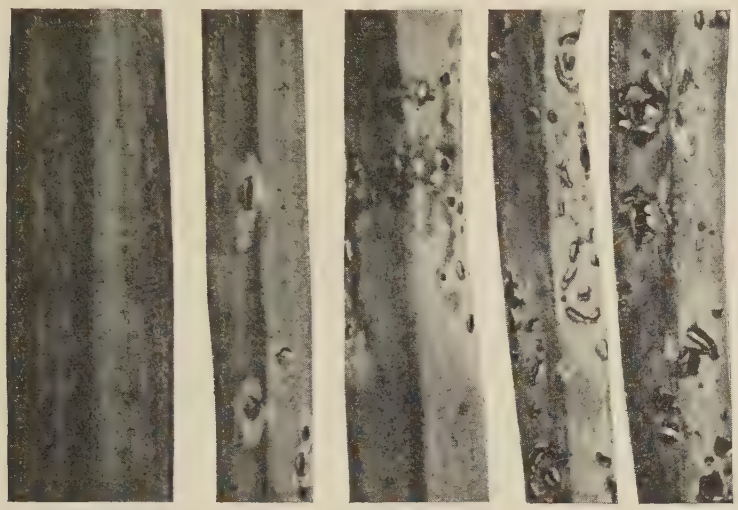


Fig. 180. — Reaction to *Uromyces caryophyllinus* shown by different varieties of carnation: *a* White Matchless, highly resistant; *b* Surprise, moderately resistant; *c* White Enchantress, very susceptible. (After Mains, 1926b.)

the industry, but it was soon learned that it could be held in check by proper cultural practices, and the disease is no longer feared by the careful grower.

Carnation rust is heteroecious with aecia on Tithymalus, but the aecial stage is known only in central Europe. The rust is spread from plant to plant solely by the urediniospores.

The early efforts to control this disease were by spraying (Stuart, 1894, 1895; Stewart, 1896), but were only partially successful. Spraying is still occasionally practised, using potassium sulphide, or weak solutions of either copper sulphate or Bordeaux mixture (Grove, 1913b).

It has been found that the urediniospores will not germinate in a

saturated atmosphere, but only in liquid water, hence any method of watering the plants so that wetting the foliage will be reduced to a minimum, or any method of handling the crop which will facilitate rapid drying of the foliage after watering, will be effective in holding the rust in check.

There is evidence that physiologic forms are to be found in Europe (Fischer, 1910, 1912, 1913). Whether more than one form occurs in America has not been determined. Considerable difference in the relative susceptibility of varieties (Fig. 180) has been noted (Mains, 1926b). The ones in general favor at the present time are relatively more resistant than those which were formerly cultivated. While little direct effort to obtain resistant varieties by breeding has been attempted, relative resistance has come to be considered a desirable character in selecting new varieties for introduction.

Chrysanthemum rust. — The rust of the cultivated chrysanthemum, *Puccinia chrysanthemi*, appeared almost simultaneously (p. 172) in Europe (1895) and America (1896) having been presumably imported from Japan (Arthur, 1900a; Roze, 1900; Jacky, 1900, 1903; Kusano, 1908). Under favorable conditions this rust is capable of causing considerable damage especially in greenhouse culture. In Europe and America the rust is known only in the uredinial stage. Teliospores occur in northern Japan, but the full life history has not yet been worked out.

While spraying has been recommended as a means of control it is ordinarily not necessary to resort to such measures. In northern regions the rust does not persist on garden plants, and by proper sanitary precautions in the greenhouse the rust is rarely troublesome.

Hollyhock rust. — One of the most conspicuous of the rusts attacking ornamental plants is the one, *Puccinia malvacearum*, which causes a serious disease of hollyhocks. This disease attacks the foliage, petioles, stems and flower bracts. When the rust is severe the foliage drops prematurely, the plants are stunted and rendered unsightly and may even be killed. The rust is native of western South America and from there has spread to all parts of the world (p. 176). Besides the hollyhock a large number of related malvaceous hosts are attacked, notably the common garden weed, *Malva rotundifolia*. The spores of this microcyclic species are capable of germination as soon as formed, and a large number of generations may be produced in a season. Spores maturing late in the fall in temperate regions are often capable of resting over winter and germinating in the spring (Taubenhaus, 1911; Eriksson,

1921). The rust may also overwinter as mycelium from late fall infections.

Spraying with weak potassium permanganate or copper fungicides, as well as the use of dusts, has been recommended. There is some evidence that resistant varieties may be obtained in due course of time.

Rose rusts. — A common rust of garden roses, *Phragmidium disciflorum*, is found throughout the world. It is especially in evidence on the hybrid perpetuals and other derivatives of *Rosa canina* and *R. gallica*, but is less likely to attack the climbing roses, especially the derivatives of *R. multiflora*, of the crimson rambler type.

The aecia, uredinia and telia are equally harmful to the foliage. In some seasons severe defoliation ensues and the plants are greatly weakened. If the rust appears early in the season, spraying with Bordeaux mixture or other fungicides frequently proves beneficial. Clean culture when it destroys the fallen leaves will tend to diminish the rust in the following season.

Other species of Phragmidium occur on wild roses and sometimes also are found on garden varieties.

THE RUSTS OF FIBER CROPS

Flax rust. — A rust, *Melampsora lini*, is common on cultivated flax almost everywhere that it is grown in Europe, Asia and America, and on many species of wild flax as well. It is autoecious and attacks all green parts of the plant. When abundant the quality and quantity both of seed and fiber are reduced, sometimes entirely destroying their market value.

It has been shown experimentally that a number of races exist (Buchheim, 1915; Hart, 1926), and that the one on cultivated flax is distinct from the others. It is further evident, although not experimentally established, that physiologic forms exist. In 1907 sowings in Australia of three varieties of seed, Russian, Japanese and Calcutta, gave crops free from the rust for the former two varieties and a crop from the last that was so rusted as to be worthless (McAlpine, 1907). The variety Argentina has been found immune to all strains so far employed (Hart, 1926).

Control of the rust lies largely in the breeding of rust-resistant strains, which has been shown to be feasible (Bolley, 1906, 1907; Henry, 1926a). The rust can be diminished by burning the refuse straw remaining after harvesting, by rotation of crops, and by early seeding.

Cotton rusts. — A wide-spread rust, *Cerotelium desmium* (*Uredo gossypii*), is sometimes severe on perennial cottons, but is not often seen on cottons of the Sea Island type. Reports of the most serious injury have come from southern Nigeria, on the west coast of Africa. The rust possesses no Aecidium-like aecia, and both the uredinoid aecia and the telia are inconspicuous and rarely formed. The rust is a leaf-form, and spread by the abundant urediniospores.

Sporadic outbreaks of another cotton rust, *Aecidium gossypii*, believed to be the aecial stage of a rust on wild grasses, *Puccinia hibisciata*, has been reported from a number of localities along the southern border of the United States from California to Florida and in northern Mexico (Taubenhaus, 1917; Olive, 1917; Blodgett, 1918). It has at times caused a financial loss of twenty to seventy per cent. The first step toward control lies in the discovery and removal of the alternate host.

THE RUSTS OF FOREST TREES

Rusts of pines. — There are many species of rusts that pass part of their life-cycle upon the pines, and among them some of exceptional importance from an economic standpoint. Only the aecial stage of the hundred or so such species now recognized occurs on pines, but the alternate or sporophytic stage attacks a wide range of dicotyledonous hosts. One microcyclic species, *Gallowaya pinicola*, also occurs on pine.

The last mentioned species inhabits the leaves of *Pinus virginiana* nearly throughout the limited range of the host in the region of the Allegheny Mountains from Maryland to Tennessee. It is said also to have been found in eastern Russia. Although an inconspicuous species it sometimes causes considerable defoliation (Galloway, 1896). Its correlated macrocyclic species appears to be *Coleosporium helianthi*.

The large number of macrocyclic species inhabiting pines fall under three genera, Coleosporium, Melampsora and Cronartium, which are injurious to their hosts in the order named.

All species of the wide-spread genus Coleosporium, of which eighty have been described, presumably produce their aecia on the leaves of pines, but only about one-third of them have had their aecial and telial forms experimentally connected. All the aecia of Coleosporium are provided with a peridium and belong to the foliicolous portion of the form-genus Peridermium. The sori of many species are large and conspicuous, but rarely cause the leaves to fall, and seemingly do little injury to the trees, whether large or small.

The aecia of rusts belonging to the genus Melampsora are without evident peridia, and go to the form-genus Caeoma. Over fifty species of Melampsora have been described, one-third of which are autoecious. Of the heteroecious species only *Melampsora pinitorqua* has its aecia on pines. This species occurs somewhat sparingly in northern Europe on *Pinus sylvestris* (Scotch pine) and *P. montana*. The uredinia and telia appear on *Populus tremula* and *P. alba*. The aecia (*Caeoma pinitorquum*) attack the young pine shoots and often kill them outright but more often cause a double curvature (Fig. 156), from which comes the Latin name and also the popular name of pine-twister (p. 304). Trees under three years of age rarely survive an attack of the rust and older trees up to ten or thirteen years are much deformed by it. The mycelium penetrates deeply into the shoot and lives for several years. The habit of the rust makes it especially destructive in nurseries and young plantations (Hartig, 1894, 1900; Tubeuf, 1897; Grove, 1913b).

The aecia belonging to the species of the genus Cronartium are distributed to various species of pine, developing in the bark of branches and trunks of all ages and occasionally in cones. There are ten or twelve species of Cronartium known, all heteroecious, and these embrace some of the most important diseases attacking forest trees. The aecial mycelium of all the species is perennial, and may form aeciospores from the same infection many years in succession.

Propagative possibilities of the rust are further enhanced by the unique feature, not known in heteroecious species of any other genus of rusts, by which the aecia of certain species produce repeating spores. By this means the rust may spread from one pine tree to another without the intervention of the alternate host, thus greatly multiplying its capacity for harm. The species now known to have this characteristic are a form not distinguishable from *Peridermium harknessii*, occurring on *Pinus attenuata*, *P. contorta*, *P. jeffreyi*, *P. ponderosa*, and *P. radiata*, in the western United States (Meinecke, 1916, 1920), and *Peridermium pini* on *Pinus sylvestris* in central Europe, whose alternate host is not known (Haack, 1914; Klebahn, 1918). A bark form on *Pinus sylvestris*, recently brought to light in northeastern New York (York, 1926), also possesses this characteristic. The gall is somewhat like that of *Peridermium cerebrum*, but the species appears to be undescribed, and the alternate form is unknown. The possible spread and injury by this species, under the name of "Woodgate rust," has become so threatening that the state of New York has been quarantined by the U. S. Department of Agriculture against shipment across its borders from the infested

areas of *Pinus sylvestris* and ten other species of hardwood pines, none of which is native to the region.

By far the most important rust attacking pines, and probably the most important of all the forest tree rusts, is the white-pine blister rust, *Peridermium strobi*. It is the aecial stage of *Cronartium ribicola*, whose alternate form is found on various species of Ribes and Grossularia, all often listed under the genus Ribes.

The white-pine blister rust is not a native of the United States (p. 172), where the most extended investigations have been conducted (Spaulding, 1922), but was imported from Europe on seedlings of *Pinus strobus* during the years between 1898 and 1908. The rust is presumably Asiatic in origin, and the native host is considered to be *Pinus cembra*, or some of its Asiatic varieties. It was first reported from the Baltic provinces of Russia in 1854. By 1883 it was well spread over Europe, though not appearing in England until 1892.

In America this rust was originally introduced into a number of localities and now occurs quite generally throughout New York, northeastern Pennsylvania and the New England States and adjacent Canada, in a limited area adjacent to the Wisconsin-Minnesota state line, in southern British Columbia, and in Washington and Oregon near the coast. These localities embrace the larger part of the most important regions for the five-needle pines in North America.

In Europe this rust is wide-spread, both on the pines and on Ribes, and the white-pine forests are threatened with extinction particularly in Norway where the planting of white pines has been largely abandoned. In some of the state forests of Denmark trees of all sizes have been killed or are slowly dying (Boyce, 1926). In southern Europe the white-pine forests are believed to be doomed, and the native *Pinus peuce*, the only immune five-leaved pine available, is recommended to take its place (Tubeuf, 1928). That the rust might cause similar destruction in America was voiced in a timely warning by an English writer, who said that "it is to be feared that the day is not far distant when it will gain a footing in North America, and if it spreads there as it has done in Europe, the loss that will result can only be described as appalling" (Somerville, 1909). The prediction has been realized.

Cronartium ribicola develops its aecia on the branches and trunks of various species of five-needle pines, the chief of which is *Pinus strobus*. Uredinia and telia occur on various species of *Ribes*, notably the cultivated black currant, *Ribes nigrum*. Infection of the pines occurs through the young leaf-bearing twigs, and the first aecia appear the

second or third spring after infection. After the aecia are mature and the aeciospores are disseminated the affected bark dies, except at the margin where the mycelium remains active and slowly spreads. The following season a new crop of aecia is developed. In this way large cankers are produced, which may extend for two or more feet on the trunk of larger trees. Such cankers may girdle the trees and the tops above die. In this manner trees of any age may be killed. Aeciospores can be carried long distances under favorable conditions (p. 166), although the usual extent of spread from pine to Ribes and from Ribes to Ribes is not great. As new infections cannot develop on pine except in the vicinity of rusted Ribes, the principle of control centers in the elimination of susceptible species of Ribes from the vicinity of five-needle pines.

The forest situation some time since appeared so serious in America due to this rust, that the Congress of the United States appropriated approximately a quarter of a million dollars annually for its extermination. When that was found impossible the effort was directed toward its control, especially by the eradication of Ribes bushes in the regions where the aecia have appeared. The most susceptible species of Ribes are cultivated in gardens and can be easily located, while many of the wild species are not very susceptible. By the method of eliminating the most susceptible alternate hosts it is now hoped that in North America it will be possible to hold the disease in check in the localities where it is established and greatly to limit the spread to new areas from the present centers of infection (Spaulding, 1911, 1922; Rankin, 1918; Pennington, 1925; Spaulding & Gravatt, 1925, 1926).

The rust of pines standing second in commercial importance is *Peridermium cornui* on *Pinus sylvestris* (Scotch pine), the aecial stage of *Cronartium flaccidum*. The alternate stage develops on a large number of herbaceous angiospermous hosts belonging to seven widely separated families. It is one of the few important rusts with a highly omnivorous habit. Although found throughout Europe and extending eastward through Siberia as far as Japan, the most injury occurs in central Europe. In northern Germany, where it is sometimes given the common name of "dry tip" or "resin tip," it is especially common in pure stands of the Scotch pine, showing on 40 to 50 per cent of the older growth and as high as 80 to 90 per cent of the younger branches. In a seventy-year-old forest 65 per cent of the trees were found to be affected. Beside the direct injury by causing the death of the ends of branches, the fungus provides an easy entrance for bark beetles and for certain wood-destroy-

ing fungi (Neger, 1924). This species has not been detected in North or South America.

Probably part of the damage ascribed to this rust is really due to another and almost indistinguishable form, *Peridermium pini*, which is common in Germany, France and Britain on *Pinus sylvestris*. Although much effort has been expended, the alternate stage of this rust has not been discovered. Its great capacity for harm lies in the readiness with which it can pass from pine to pine without the intervention of any other than the one form of spore (Tubeuf, 1897; Klebahn, 1918).

A blister rust, the aecia of *Cronartium harknessii*, abundant upon a number of species of pines in the Rocky Mountain and Pacific Coast regions, causes considerable economic loss. It appears in three forms, which may constitute races, and for a time were considered separate species (Arthur, 1922a).

Of the three forms *Peridermium filamentosum* occurs on twigs and smaller branches and rarely on trunks, without causing perceptible swelling. The aecia are usually cylindric, distinct, and have noticeable filaments extending through the center. *P. stalactiforme* causes little or no swelling and often extends over considerable areas of bark. The aecia are low and flat, with a circumscissle dehiscence, and have only rudimentary filaments. The third form, originally described under the name, *P. harknessii*, makes conspicuous globoid swellings, which may reach one or two feet in diameter on the trunks of large trees (Fig. 77). The aecia are flat and coalesce, so that the peridium often falls away in large flakes (Fig. 16a). There are no filaments. All of these forms have their alternate stage on species of Castilleja, Pedicularis, Orthocarpus, and other scrophulariaceous genera.

The injury to young trees in the nursery is often great, either killing them outright or stunting the growth. The large woody galls on the trunks or limbs of older trees, especially on the yellow pine, *Pinus ponderosa*, and the lodgepole pine, *P. murrayana*, may occasion the death of a part or all of the tree (Hedgcock, 1912, 1913; Meinecke, 1916, 1920; Weir & Hubert, 1916, 1917).

Another bark rust of pines, *Peridermium cerebrum*, is the aecial stage of *Cronartium cerebrum* (*C. quercus*), and is common in its globoid form (Fig. 165b) on a number of species of pines in the northern United States east of the Rocky Mountains. It occurs on trees of all ages and produces galls up to eight or ten inches in diameter. The galls continue to develop slowly; a single gall on the trunk of *Pinus divaricata* has been known to remain alive fully 75 years. In the National Forests

of Michigan half of the trees and sometimes all of them over considerable areas were found to bear one or more galls (Graves, 1914; Weir, 1915). Beside the familiar form with a globoid gall there is the form (Fig. 165a) with a fusiform gall, *P. fusiforme*, occurring southward, especially on branches and trunks of *Pinus taeda* (Hedgcock & Long, 1914).

There is also a cone form, or possibly two forms, that appears to belong to the same species of rust. One occurs in Florida and Mississippi on *Pinus heterophylla* and *P. palustris*. Young cones are infected early in the season and become permeated by the mycelium and much hypertrophied. By autumn the diseased cones are dead. In 1919 from 25 to 90 per cent of the total crop of cones upon an area of two acres were found to be diseased. Even cones on trees a hundred feet or more tall are affected. The aecia are sunken deep into the tissues and the peridium remains more or less deeply buried, and easily overlooked, so that at first the fungus was thought to have no peridium and was referred to the form-genus Caeoma, and given the name *C. strobilinum* by Hedgcock and Hahn (1922). In southeastern United States and Mexico is a similar cone rust, probably a form of the same species, on other species of pines. It was at first given the name of *Caeoma conigenum* (Hedgcock & Hunt, 1922).

These several diverse forms are sometimes treated as distinct species. They produce uredinia and telia on various species of oaks, and in the present status of knowledge their taxonomic relationship is best expressed by considering them races of *Cronartium cerebrum*. What appears to be the same rust in globoid form, and may constitute another race, occurs over a limited area on the Pacific Coast south of San Francisco, California, especially on the Monterey pine, *Pinus radiata*. But the identity of the form in this region is yet in doubt. A tree of *P. radiata* 6 inches in diameter at base and 12 feet high was observed to bear as many as 529 galls (Meinecke, 1916, 1920).

The aecial stage of *Cronartium pyriforme* is found on a number of species of pine in considerable abundance in the northern United States and adjoining Canada, and produces injuries of much importance. It is especially destructive to young trees, favored by the low-growing alternate hosts, species of Comandra, which are usually only about a foot tall. Little or no swelling of the pine branch is produced, but the fungus frequently girdles the stem and causes its death. The unique form of the aeciospores, pear-shaped and often pointed at the narrower end, gave the suggestion for the specific name (Arthur & Kern, 1913; Hedgcock & Long, 1915a, b).

Another rust, similar in behavior and destructiveness to *C. pyriforme*, occurs in the Atlantic States from North Carolina northward into Canada, and sparingly westward into the Mississippi Valley and in northern California. This rust, *Cronartium comptoniae*, attacks a number of two- and three-needle pines, and passes to species of Myrica and Comptonia for its sporophytic stage. As a rule only young trees are injured, often resulting in their death, and in consequence nurseries suffer most noticeably (Clinton, 1908; Orton & Adams, 1914; Spaulding, 1913, 1917). It has been found especially destructive to western pines introduced into the east (Rhoads, Hedgcock, Bethel & Hartley, 1918).

The piñon pines, *Pinus edulis* and *P. monophylla*, are hosts for another blister rust in the Rocky Mountain region. This species, *Cronartium occidentale*, while not a serious disease of the pines, is of interest because the uredinia and telia occur on Ribes, and the species was for a long time confused with *C. ribicola* (Hedgcock, Bethel & Hunt, 1918; Colley, Hartley & Taylor, 1927).

The rusts of firs, spruces, hemlocks and larches. — A large number of leaf and cone rusts find congenial hosts among the several species of these coniferous genera. With rare exceptions (p. 302) none of the forms is of much economic importance, as the mycelium is usually confined to individual leaves or to the scales of the cones. All the species, so far as known, are aecial stages of heteroecious rusts with the exception of two microcyclic species, *Chrysomyxa abietis* on Picea and *Necium farlowii* on Tsuga, which are correlated with the genera Melampsoropsis and Melampsora respectively, and two on Picea, *C. weirii* and *C. piceae* of uncertain affinity. The rusts of this group are found in all parts of the world, but especially northward. The aecia are partly with and partly without a peridium, and belong to the form-genus Peridermium or Caeoma, with one exception, *Uredo holwayi*. The alternate form of this unique rust is unknown. It is a true aecium, although characteristically uredinoid, and affects the host in the same way as other aecial forms. It occurs on *Tsuga heterophylla* and *T. mertensiana* in the mountainous districts from Idaho and Montana northward into Alaska.

The genera to which the aecia of this group have been assigned, and the number of species in each, are as follows: for the firs (Abies and Pseudotsuga), Calyptospora 1, Hyalopsora 1, Melampsora 2, Melampsorella 2, Milesia 2, Pucciniastrum 2, Uredinopsis 4; for the spruces (Picea), Melampsoropsis (Chrysomyxa) 4, Pucciniastrum 2; for the hemlocks (Tsuga), Melampsora 1, Pucciniastrum 2; for the larches (Larix), Melampsora 7, Melampsoridium 1; making altogether 31

species whose life histories are known. There are many species whose life histories are not known. The sporophytic stages are on many kinds of hosts from diverse herbaceous plants, including ferns, to shrubs and trees.

Little injury to the coniferous host is caused in general by these fungi, beyond hastening the shedding of some of the leaves and in the cone forms the abortion of some of the seeds. Epidemics are exceedingly rare even over a limited region.

In the few cases where the mycelium penetrates the tissues of the stem somewhat greater injury is done to the host. In *Peridermium coruscans*, found on spruces in northern Scandinavia and Russia, the infected buds produce short, pale, and much hypertrophied shoots (Fig. 155). In *P. elatinum* (Fig. 170) on firs in Europe and America, and the similar *P. coloradense* on spruces in America, the infected branch becomes a pale and conspicuous witches' broom, which may increase to two feet or more in diameter and persist many years (p. 311). The branch on which the witches' broom occurs is usually much enfeebled, and the portion beyond the witches' broom often dies (Hartig, 1894; Tubeuf, 1897; Hedgcock, 1912).

CHAPTER X

METHODS OF INVESTIGATION

Collection and preservation: significance of herbaria; collecting, making specimens, preservation of material; arrangement of collections.

Technic for microscopic study: general methods, use of reagents and heat, stains, measurements, counting pores, surface markings, permanent mounts, free-hand sections; cytologic methods, fixing material, embedding, stains, sectioning.

Culture work and methods: source of inoculum, testing spores for germinability, methods of inoculation, inoculation chambers, cultures upon detached branches or leaves, isolation of pure strains, exclusion of other fungi, recording laboratory results; field cultures, recording field results.

COLLECTION AND PRESERVATION

Significance of herbaria. — The collection of specimens is an important factor in connection with the study of rusts, as it is with most other groups of plants. An adequate knowledge of the nature and distribution of the rust-flora of the world or of any large portion of it is dependent on abundant collections carefully preserved and deposited in herbaria, where they may be properly cared for and are readily accessible.

Collecting. — The successful collector of rusts, when in the field, keeps an eye on practically all vegetation, looking especially for discolored spots, swellings or galls, and leaves or shoots which are more upright than usual or otherwise changed in position, but does not fail to take hold of and inspect closely many plants which appear perfectly normal and healthy, especially by turning over the leaves, as the majority of foliicolous rusts make their appearance on the lower surface (Kern, 1913). Passing the leaves lightly between the fingers is helpful, as most kinds of rusts break through the surface of the plant and make it rough, while most other microfungi do not. A hand lens is highly serviceable in forming a judgment as to the presence of a rust. A microscopic examination must be the final test in some cases, however, for gross appearances and even the appearance under a hand lens may be misleading, especially where there is persistence of overlying host-tissue. Attention should be given to the stage of the rust. It is especially

desirable for macrocyclic species to have both gametophytic and sporophytic stages included, even if one of them is scanty and in the very early or very late period of its development. For known or suspected heteroecious species the alternate form should be kept in mind (Arthur, 1902c).

Making specimens. — The gathering of a fair amount of material is essential. Altogether too many important collections and especially early ones are fragmentary. There seems to be some natural association in the minds of most collectors between the minuteness of material required for a microscopic examination and the quantity of material required for a practical study of the rust. It is not enough, however, that one is able to examine the spores, for it is often quite as important to see the variation in appearance of the sori on different parts of leaves or stems, or even to study the identity of the host. In the case of a leaf-inhabiting form a specimen consisting of less than a dozen well-affected leaves can rarely be considered ample.

Some knowledge of hosts is required of one who would be a really successful collector of rusts. The importance of collecting parts of the host-plant to aid in its determination cannot be over-emphasized. Sometimes not only verification of the identity of the host is required, but means should be provided for a restudy of the material in order to follow up a revision of the group to which the host belongs. Flowers or portions of the inflorescence, portions of the stem, bark, unrusted leaves, basal leaves, etc., are advantageous. It is especially desirable to secure such parts as are most utilized for classification, as inflorescence showing mature perigynia in Carex and mature fruits in umbellifers, the base of the leaves showing auricles in Juncus, the burs for Xanthium, bulbs for Allium, etc. Careful attention must be given to securing only such parts as come from the same plant that bore the rusted specimens, or at least from the same species. Carelessness in this matter has been responsible for some curious and unfortunate results.

Some collectors make separate phanerogamic collections for host determination, which is especially desirable in regions where the phanerogamic flora is not well known, but is not necessary as a rule, and is often less satisfactory and convenient than the inclusion of smaller diagnostic portions of the host along with the fungous specimens.

Preservation of material. — Most specimens can be prepared for the herbarium by lightly pressing them between some sort of absorbent driers after the ordinary method employed for phanerogams. Since spores can be transferred from one specimen to another through the

medium of the driers and thus bring about situations which are misleading, it is better to protect the driers with tissue paper, or else employ driers which can be discarded after once using, such as newspapers.

The place and date of collection and the collector's name are essential. Additional data regarding habitat, altitude, etc., make the collection more valuable.

A serial number is desirable when many specimens are taken by the same person, or in the same region. Such numbers need not be consecutive, the only requirement being that there shall be no duplicate numbers. If phanerogamic specimens like the host of the fungus are collected at the same time, they may bear the same number. Some collectors use a separate series, or designate the fungi by attaching a letter to the number, but one number for both host and parasite has been found most serviceable. As the sole purpose of a number is readily to identify the material collected in one place, at one time, and on the same host, however many times that material may be subdivided, the numbers to avoid errors should be attached at the time of collection, or when the material is placed between driers. As a number does not imply that the preceding numbers represent collections, it is best to begin a series with numbers of two or more digits.

Arrangement of collections. — Specimens are kept best in mycologic packets which may vary in size according to the character of the material. Packets are made in various forms, but should be of sufficiently firm paper and be folded in such a manner that they do not easily spread open and permit the loss of the contents.

In some places packets of uniform size are used and stored in drawers in the card-index style. With this plan genera and species are usually arranged alphabetically. It is a method that has advantages in way of ready reference and easy expansion, but does not permit of the insertion of extra large specimens.

Another plan preferred by many, especially for extensive collections, is that of mounting the packets on herbarium sheets of regulation size, $11\frac{1}{2}$ by $16\frac{3}{8}$ inches (29 by 42 cm.). Such sheets can be placed in genus covers and stored in herbarium cases after the manner of a phanerogamic herbarium. Restricting the specimens on a sheet to a single species of host as well as a single species of rust is most satisfactory, and greatly facilitates their arrangement. It is also possible by this method to mount drawings or photographs beneath the packets, or to make notes on the sheets, and thus have them in a convenient place for ready reference and study (Fig. 181). If the packets are attached with library

paste, or some adhesive containing little or no glue, the packets can be removed without tearing the paper, should a rearrangement be desired. Sometimes sheets of half the regulation size are used. If specimens are too large or thick to be mounted on the sheets, they may be placed

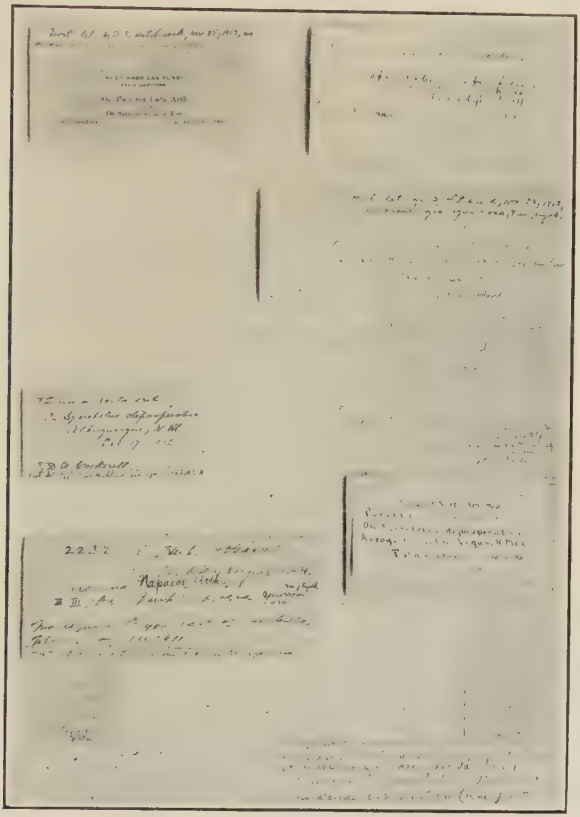


FIG. 181. — Herbarium sheet with packets of rusts, illustrating the method of mounting and attachment of drawings, notes and photographs. (Original.)

in boxes of multiple sizes that fit into a covered box of the length and breadth of the herbarium sheet, and of such depth as may be desired. Such boxes may be placed in their appropriate places in the herbarium.

An arrangement of the genera according to some generally accepted system of classification lends itself to the situation where considerations of relationship are a matter of interest. The species under each genus may be arranged alphabetically or by families of the host. The latter

method assists in bringing related species together, and changes in the name of the rust do not affect the position of the specimen in the herbarium. Some persons prefer an alphabetical arrangement both of genera and species, which facilitates reference. There is no generally accepted method of arranging or classifying a herbarium of this kind.

An important adjunct to a herbarium, especially designed to conserve scanty collections and others that might be injured by too frequent removal of spores, is a cabinet of mounted slides (Holway, 1902). The spores are mounted dry, or in distilled water which is allowed to evaporate, and the cover-glass is fastened in place with a narrow strip of gummed paper. The number given to the slide is also placed on the packet from which the mount is taken. The slides are readily available for study of surface markings of the spores, or by adding a drop of distilled water for other details. Such preparations usually may be kept and reused indefinitely.

TECHNIC FOR MICROSCOPIC STUDY

General methods. — The spores of the rusts, whether dried or fresh, can be prepared for microscopic study as a rule by mounting in water on the ordinary slide with cover-glass. If distilled water is employed, it is possible to allow a slide to become dry and when again needed for examination water can be run under the cover-glass, and fair results secured.

Fig. 182. — An electric hot-plate for heating microscope slides and boiling material for sectioning.

When spores are taken from old specimens they sometimes do not wet easily, or they may appear shrunken. A good treatment in such cases is the addition of a little lactic acid to the drop of water. This will cause the spores to round out and take on a fairly normal appearance. If the fluid of the slide is heated to the bubbling point the action of the acid is hastened (Fig. 182). By adding a drop or two of potassic hydrate to the slide, with or without the lactic acid, both spores and sections are made much clearer. With such treatment the elements of a sorus can often be separated by gentle pressure on the cover-glass, or by teasing apart with needles. Preparations so treated cannot be preserved for future study.

Lacto-phenol is considered better than lactic acid, as it does not

crystallize, and can be used for permanent mounts. It is prepared by mixing equal parts of lactic acid, phenol, glycerine and water.

Still better results can be secured, especially in showing pores, by using a 10 per cent potassic hydrate to which enough Grübler's benzoazurin, or Niagara blue G (manufactured by the National Aniline and Chemical Company) is added to produce a wine color. The slide should be heated. Other stains are found serviceable in particular cases. Success in the use of reagents or stains will often depend upon the detail and nicety of manipulation.

The range of measurements given for spore-sizes is customarily based on the average of some ten or twelve individual spore-measurements. The larger the number of measurements taken, and the judgment shown in selecting the range of representative spores, the more accurate the results. In the hands of some workers (Levine, 1923; Bailey, 1925; Colley, 1925) comparisons in spore-size by the use of biometric constants, calculated according to standard methods, have yielded interesting and exact results. In special cases the use of these constants may be an important factor in determining identity and relationships. In all cases when measurements are being made, care must be taken to have the spores properly oriented so that the longitudinal axis lies at a right angle to the line of vision.

The thickness of spore-walls can be measured without difficulty when the walls are naturally colored to a moderate degree. If the wall is too deeply colored, lactic acid will serve as a clearing agent. If the wall is so light in color that its exact thickness can not be readily ascertained, the use of chloral-hydrate-iodine stain is likely to be helpful (Rosen, 1918). It is prepared by dissolving five parts of chloral hydrate in two parts of water and adding enough finely powdered iodine to leave an excess undissolved after long standing (Stevens, 1910). Alcohol in the mounting medium may be required to prevent undue swelling of walls which have a gelatinous layer.

In counting the number of pores in urediniospores care must be taken not to mistake the hilum for a pore. The hilum is the scar left by the falling away of the pedicel, and often has the size and gives the appearance of a pore. Recognition of the hilum in globoid or ellipsoid spores aids greatly in deciding upon their orientation. It may be necessary to rotate the spore by moving the cover-glass in order to complete the observation as to number and arrangement of pores. By changing the focus it is often possible to tell whether a pore is in the upper or lower wall.

Lactic acid or lacto-phenol will assist in making pores more evident in dense walls, and a stain is equally helpful in bringing out the pores in faintly colored walls. The pores can frequently be made visible in thin colorless walls, like those of the urediniospores of Uredinopsis and Hyalopsora, by heating for a minute or more in dilute lactic acid, but for the thin echinulate urediniospores of some of the Pucciniastreae, and others of like character, much more prolonged boiling may be required.

Surface markings and sculpturings are usually not difficult to make out. When they are faint or questionable the examination of the dry spores without a cover-glass is helpful for comparison. Surface markings may often be rendered distinct by mounting spores in a small drop of water to which has been added some lactic acid, and then heating the slide gently until the liquid evaporates. By this method the contents are made clear, the wall is not shrunken, and the markings are surrounded by air and are plainly visible.

The surface elevations which are rounded and wart-like are said to be verrucose, and when much broader than high, particularly if large and irregular, are called tuberculate. When the surface elevations are pointed or prickle-like they are described as echinulate. Qualifying terms such as close, moderate, or sparse are used to indicate the distances apart of the markings (Rosen, 1918).

On account of the ease and satisfactory results in making spore-mounts in water from either fresh or dried material the occasion is rare in taxonomic studies for attempting permanent mounts. Glycerine jelly and Canada balsam are useless as mounting media for the spores of rusts, for the spores become swollen and decolorized in time. Some success has been obtained in securing permanent mounts by using lacto-phenol (p. 368), Merk's glycerine with King's cement, or something similar.

Sections are desirable for studying the structure of sori. With some practice good free-hand sections may be made in pith, which will serve a very definite purpose. If the specimens are dry, small bits of the material should be selected and thoroughly soaked, or preferably boiled in water (Fig. 182). To hold the material while sectioning pith soaked in alcohol is better than dry pith, and it is an aid to float the razor blade with alcohol or water. When prepared in this way the sections are ready for immediate examination. Sections mounted in distilled water may be allowed to dry out and then be remoistened and examined with fair results. The addition of alcohol to the slide will help to remove inter-

fering air bubbles. The details of the structures can be much better seen if a drop of lactic acid or potassic hydrate is added and warmed to the boiling point, which, however, will prevent keeping the slide for reëxamination.

Cytologic methods. — Although many features of rust structure may be studied adequately from hand sections it is necessary to use microtome sections for the more intimate details. The usual methods of killing, fixing, embedding, and staining are applicable to rust materials generally, but some adaptations and precautions are useful in special cases.

Many investigators emphasize the necessity or desirability of fixing material in the field. For this purpose small specimen or shell vials holding about 2 ccm. of the fixing fluid are especially serviceable. A piece of leaf about 2 or 3 mm. square, bearing a selected sorus, may be dropped into each container. As the washing and after treatment can be done best in a laboratory, the vials with their contents can be transmitted through the mail, even over distances requiring several days. When transportation of material need not be considered, more pieces of the host can be placed in correspondingly larger amounts of the fixing fluid.

Flemming's fixative, in either weak, medium, or strong solutions, seems to be a favorite. In some cases where there may be a strong affinity between the osmic acid and some substance in the host-tissue it may be essential to use a considerable quantity of the fixing solution (Adams, 1919). Chrom-acetic fixing fluid, which is similar to Flemming's but without the osmic acid, has been used by some investigators with highly satisfactory results (Moss, 1926). Chrom-acetic-urea has given excellent results particularly with leaves of cereals (Allen, 1923b, 1926b). Picro-sublimate, Merkel's and Bouin's fixatives have been experimented with by some workers. Other modifications for the study of nuclear changes in spores are suggested by Chamberlain.[1] Difficulty in fixation due to slow penetration has in some cases been obviated by placing material during fixation in a cold-storage chamber at a temperature of 4° to 7° C. (40° to 45° F.). Material of cereal rusts fixed in the cold is considered superior to that fixed at room temperature (Allen, 1926b).

For the most part dehydration, infiltration, and embedding are carried out by the usual cytologic methods. The paraffin process has been used almost exclusively for leaf and bark tissues. For the latter

[1] Chamberlain, C. J. Methods in plant histology. 4th ed., 343 pp. 1924.

it may be necessary to keep the specimens in the paraffin bath for several days to insure perfect infiltration. In such genera as Peridermium and Gymnosporangium where woody parts are encountered the celloidin method has been employed, sometimes including the hydrofluoric acid treatment (Colley, 1918).

Flemming's triple stain, safranin-gentian violet-orange G, is generally mentioned as giving the best results for cytologic studies. Heidenhain's iron-alum-haematoxylin is frequently suggested as useful for comparison, and safranin and light-green used in combination have proved satisfactory in the hands of some investigators.

To differentiate fungous mycelium and host-cells various combinations of stains have been tried. Alcoholic safranin and gentian-violet dissolved in clove-oil are particularly good for mycelium in the xylem, while Delafield's haematoxylin followed by erythrosin in 70 per cent alcohol is best for mycelium in the phloëm or cortex (Colley, 1918). Flemming's triple stain gives excellent results in bringing out mycelial and host relations at the base of sori, the active basal cells of the fungus taking the gentian-violet stain rather deeply (Colley, 1918; Dodge, 1923b). For differentiating the mycelium in rhizomes and hibernating buds a solution of aniline blue in lactic acid (0.1 gram to 50 ccm., with 100 ccm. water) has been found effective, especially with hand sections. Place the sections in the stain for five minutes, rinse in clear water, mount in a drop of weak lactic acid and warm (Kobel, 1920).

Sections may be cut both transverse and parallel to the surface of the host. The latter are especially useful in the study of mycelium. Where continuity of cells is especially desired, as in studies of the nuclear content of hyphae, masses of the mycelium may sometimes be teased out of the host-tissue and stained *in toto* (Bartholomew, 1916).

The details of nuclear behavior during spore germination may be studied by attaching the spores to slides with egg albumen, after which they are fixed, hardened in alcohol, and stained. A better method is to use an extra thin cover-glass coated with a very thin layer of agar, over which spores are dusted. The cover-glass is laid in a moist chamber for a time, varying from one to several hours, to permit germination. The preparation is then flooded with Flemming's fixing solution, washed, hardened, and stained with acid fuchsin and iodine green. The loss of some spores will usually prove no detriment (Dodge & Gaiser, 1926).

CULTURE WORK AND METHODS

Importance of culture studies. — Future investigations of rusts in many of their aspects must involve experimental studies by means of cultures. Culture work is required for the advancement of knowledge regarding life-histories, heteroecism, and physiologic specialization.

The methods essential in culturing rusts are for the most part simple. Early investigators merely exposed plants to infection from spore-bearing plants. Not understanding the relation of spore germination to temperature and moisture their results were to some extent erratic. Since the demonstration of heteroecism by de Bary, and the specialization into races and strains by Eriksson, investigators have developed more intensive and detailed lines of study, necessitating certain refinements. The recent discoveries by Stakman and his co-workers of the existence of extreme specialization of strains of *Puccinia graminis*, which develop well only upon certain varieties of wheat, have emphasized the necessity of still greater refinements.

For the most part, descriptions of methods employed are scattered through mycologic literature in papers on different phases of rust investigation. Only a few papers have been written primarily dealing with culture methods (Carleton, 1903; Kern, 1906; Melhus, 1912; Fromme, 1913; Rosen, 1918; Klebahn, 1923; Mains, 1924a). An attempt will be made here not only to describe the methods in general use but also to indicate such modifications or innovations as show promise of further usefulness.

Unless otherwise specifically stated, cultures in recent times are understood as conducted under laboratory conditions, usually in a greenhouse, and in such manner as will permit the control of growth conditions for the host-plants used and the least danger from spore contamination.

Source of inoculum. — Where the problem involves only the study of a rust occurring locally, to obtain inoculum is relatively simple. Usually plants bearing the rust desired can be secured from the field over fairly long periods. Sometimes it is possible to lengthen the usual period by successive plantings of the host. Under these conditions the inoculum is available in fresh and germinable condition.

When the problem involves the study of rusts from distant localities, greater difficulties are encountered. However, if properly handled, material for cultural studies can be successfully transported long distances. Such material should not be covered with wet cloth or cotton

or wrapped with oiled paper, with the idea that it is necessary to prevent the material from drying out. Under such conditions, especially during hot weather, more or less fermentation, molding, and heating is likely to result, which is highly detrimental to the germinability of the spores. It is better after collecting the required portion of the rusted plants to place the material in ample Manila envelopes, with the data written on the packet. Such a packet can be mailed without additional wrapping. Usually such material, although the host may be much wilted, will be received with the spores in germinable condition, even when sent long distances. It is desirable that aecia especially be thoroughly mature in order that the spores may be in condition for culturing.

It is often required that inoculum be kept in germinable condition for some time, either until the proper host is available, or to check up on first culture results by further sowings, or to carry the culture over conditions adverse to good rust development, as in the hot summer months. Aeciospores and urediniospores under low temperatures and moderate humidities usually retain their viability for considerable periods. Advantage may be taken of this fact by storing spores in a refrigerator, either on the material as gathered and preserved in envelopes, or removed and placed in vials or gelatine capsules (Fromme, 1913; Melhus & Durrell, 1919; Mains, 1924a). The longevity of such material will depend upon a number of factors (p. 222).

Although, in general, aeciospores and urediniospores are germinable when they are readily detached from the spore-chain or pedicel, yet in some species such spores give a very low percentage of germination, and apparently require a period of after-ripening (p. 220). Occasionally greater germination can be obtained by allowing the spores to dry for a few days before sowing. The aeciospores of a few species, as for example, *Gymnosporangium juniperi-virginianae* (Weimer, 1917a) and *G. yamadae* (Fukushi, 1925), often give little or no germination when freshly gathered or dried, but seem to need overwintering before becoming fully germinable.

The teliospores of many species, even more than aeciospores, require the lapse of a certain amount of time before they will germinate. The necessary changes, whatever their character may be, usually take place during overwintering. When such teliospores are to be used in culture studies it is best to expose the rusted plant-parts out of doors during the winter. The parts of the plant bearing the spores, if of firm texture, can be placed in coarse cheese-cloth bags, suitably labeled, and hung within a foot or so of the ground, where they will be subjected to

the vicissitudes of weather that naturally affect such rusts (Fischer, 1898). Another method is to place the rusted material in common flower pots, but not so much in a pot as to induce molding. Each pot, suitably labeled, is set upon an inverted pot of the same size, in order to protect the contents from earthworms, mice, winds, etc. All the pots are placed in the open on the ground where they will be subjected to the usual changes of weather, and should be protected from casualties by boards or wire-netting (Klebahn, 1904a, 1923). If the plant-parts to be preserved are of soft or delicate texture, they can be laid in flower pots containing finely sifted soil or sand, the pots covered with wire-netting, and otherwise treated as just described. As the leaves will have largely disintegrated during the winter, the surface soil or sand, into which the spores have fallen, can be used in the spring as inoculum.

By testing the overwintered material at intervals during the spring the spores may be sown when found to be in good germinable condition. Alternate wetting and drying, or prolonged soaking in tap water, will sometimes bring resting spores to earlier germination (Klebahn, 1914; Mains, 1916; Maneval, 1922).

Testing spores for germinability. — Where there is any doubt concerning the germinability of spores used in culture studies it is advisable to test them. This is not primarily a test of viability, for many spores, especially those upon grasses and sedges, remain viable but dormant for long periods, so that under favorable conditions for germination they give no indication of germinability.

In the case of urediniospores and aeciospores it is not always essential that preliminary tests should be made, especially when dealing with fresh material. With these spores, however, if the inoculum is old or the plants upon which it is sown are uncertain hosts, it is well to make germination tests in order to give proper value to negative results. In the case of many teliospores, it is important to make such tests to determine the end of the period of dormancy.

A number of different methods for making germination tests have been employed. It is essential that the device to be used should maintain a high humidity and be so arranged that it can be placed under the microscope for observing results. The modified Van Tieghem cell, consisting of a glass ring sealed upon a glass slide, has been considerably used. By this method water is first placed in the bottom of the cell, then a drop of water is placed upon a cover-glass and the spores are added to this drop, after which the cover-glass with its drop is inverted and sealed with vaseline to the upper border of the ring. This method

has the advantage that germination of the spores can be observed even under the higher powers of the microscope without in any way reducing the humidity of the chamber. It has the objection that the small amount of oxygen contained in the cell may soon be used up, and germination thus inhibited. The use of vaseline is also objectionable, as it may stimulate growth (p. 213), and give an abnormal result.

The use of vaseline may be avoided by placing the cells in Petri-dishes. The bottoms of the dishes are covered with blotting or filter paper through which holes are cut to accommodate the cells and transmit the light. The paper is kept wet, and it is therefore unnecessary to seal the rings to the bottom of the dish or the cover-glasses upon the rings. A modification is made by placing the drop of water bearing the spores either on the upper or lower side of a glass slide, which is placed in a Petri-dish and raised above the wet substratum of moistened filter paper, by glass slips (Melhus & Durrell, 1919). This method has the advantage of a plentiful supply of oxygen, no contact with stimulating or toxic substances, and ease of preparation.

A method by which the slide and cover-glass are wholly dispensed with is to place the spores in hanging drops on the under side of the lid of a Petri-dish, the bottom of the dish being covered with water or wet filter paper (Mains, 1916; Weber, 1922). A somewhat similar method, and one requiring considerably less space, is to use Syracuse watch-glasses. Water is placed in the watch-glass and the spores floated on it, or a single drop of water bearing spores is placed in the watch-glass, which is then inverted over another in like position with water on the bottom, thus making a hanging drop in a moist chamber. The dishes, which are beveled and grooved, can be stacked one above the other and thus occupy but little space (Hursh, 1922; Mains, 1924a). Watch-glasses can be used to advantage only when examination is made under low powers of the microscope.

Agar plates are sometimes used for making germination tests. By placing the leaf bearing the sori over the agar a spore print will be obtained, and the germination of the spores from each sorus can be separately studied (Dodge, 1923a).

Germination of teliospores often takes place best if they are left attached to the substratum, or remain in clumps (p. 218). Excellent germination of teliospores of *Puccinia graminis* has been secured by placing short pieces of straw bearing the spores in vials lined with moist filter paper (Thiel & Weiss, 1920). While aeciospores and uredinio-spores will usually float on the surface of water and give good germina-

tion, teliospores, especially if still surrounded by host-tissues, are likely to sink and good germination may not be obtained. In such cases it is best to make the test in hanging drops, as the material will then be kept at the surface of the water.

If anything further is desired than merely to ascertain the germinability of the spores, it must be borne in mind that most spores do not grow in a wholly normal way when submerged (pp. 210, 292). The customary employment of a hanging drop largely accounts for the many distorted and odd forms figured by authors from the earliest to the present time.

Methods of inoculation. — The inoculation method to be used will depend upon the type of investigation. Where either a few plants are being inoculated, or the amount of the inoculum is small, or where different strains of the rust are being studied, necessitating carefully controlled conditions, it is usual to inoculate each plant with spores applied with a scalpel. If the plants to be inoculated have a waxy coating on the leaves, as with the cereals, water does not adhere well. This can be overcome by gently drawing the leaves between wet fingers (Melchers, 1915). In many cases atomizing is all that is necessary to thoroughly wet the plants. Spores, taken from rusted plants with a straight-edged scalpel, are spread on the wetted leaves.

Some investigators find it convenient to trim away all leaves from the plants used for the experiment except those inoculated, in order that there may be no confusion as to the parts infected. This is not always desirable. Usually there is no difficulty in telling the parts inoculated, but when necessary leaves or stems can be marked with India ink, a bit of string, or tagged. The part of the plant selected to be inoculated will depend upon the species. The germ-tubes of aeciospores and urediniospores enter through stomata, with rare exceptions, and consequently these spores should be sown upon parts of the plant possessing stomata.

In the case of catenulate spores, like aeciospores, it is only the upper spores of the chains which are mature, and scraping removes a large number of immature and useless spores. By loosely wrapping the plant-parts bearing aecia with paraffined paper, the mature spores will be caught and can be used as inoculum.

Advantage can be taken of the forcible discharge of basidiospores to collect them for inoculation purposes. As they are thrown off from the sterigmata they will adhere to a glass slide placed beneath, or to one placed somewhat less than a millimeter above (Melhus, Durrell & Kirby, 1920). They can be taken from the slide and used in the same manner

as other spores. The germ-tubes of basidiospores pass directly through the epidermis, and these spores may therefore be sown upon any desired part of the plant, without reference to the presence of stomata.

With some species of rusts spores may be placed in suspension in water and atomized on the plants with good results. In other species, however, the immersion of spores in water is detrimental to their normal germination, and as abundant an infection can not be obtained in this way as by other methods.

When plenty of inoculum is available, dusting with spores is an effective method of inoculation. It is a rapid and easy method, especially when large numbers of plants are to be treated. A good way to dust is to atomize the plants first and then shake heavily rusted material over them, after which the treated plants are placed in a moist chamber. Or, the inoculum may be scraped from the plants supplying the material, placed in a glass tube provided with a bulb, and then blown upon the plants to be inoculated (Durrell & Parker, 1920). Dusting has the advantage that the plants are more uniformly inoculated.

In those species where the teliospores do not readily separate from the host, the plant-parts bearing the spores may be placed directly on the plants to be inoculated, or suspended above them (Fig. 183). These methods sometimes give an added advantage, as germination of the teliospores often takes place best when attached to the host (p. 218).

Inoculation under the bark of small stems can be made by thrusting a thin and narrow scalpel blade beneath the cortical tissues, but not deep enough to reach the xylem, so as to raise a very short and narrow strip of bark, under which the spores can be inserted. The strip can be made to bulge out to allow insertion of the inoculum by bending the stem of the plant, which upon being released will bring the strip into place again. To prevent drying out bell-jars or celluloid cylinders (p. 380) can be used, no other protection of the wounds being necessary (Meinecke, 1920).

The condition of plants at the time they are inoculated has an important bearing on the results of inoculation. If a thorough test of susceptibility is desired, the plants to be inoculated should be in the best of growing condition. Plants in a wilted, senescent, or dying state may appear resistant, while if growing vigorously they might be found to be highly susceptible.

Inoculation chambers. — After plants have been inoculated with spores, it is necessary that a humidity close to one hundred per cent be maintained in order that germination may take place (p. 209). Tem-

perature also is of importance, the different rusts varying somewhat as to the optimum temperature for germination (p. 214). Since under greenhouse conditions the atmosphere is seldom saturated for any length of time, it is necessary to provide a chamber in which such a condition of the atmosphere can be maintained until the germ-tubes have emerged from the spore and entered the host.

Various types of inoculation chambers, which will provide suitable conditions, have been used by different investigators. The most common form, and one which has been in general use from the beginning of culture studies, is the bell-jar (Fig. 183). When only a few plants are inoculated this method works well. The objections to bell-jars are their expense and the ease with which they are broken. Lantern-globes have been used as a substitute for small bell-jars, the upper opening being covered wtih a thin layer of cotton-wool held in place with cheese-cloth (Mains, 1924a). Shade should be provided, since in direct sunlight the temperature inside the chambers may rise too high for optimum germination of the spores. It is well to keep the soil, sand, or sphagnum moss, on which the glass chamber rests, well moistened to aid in maintaining the humidity.

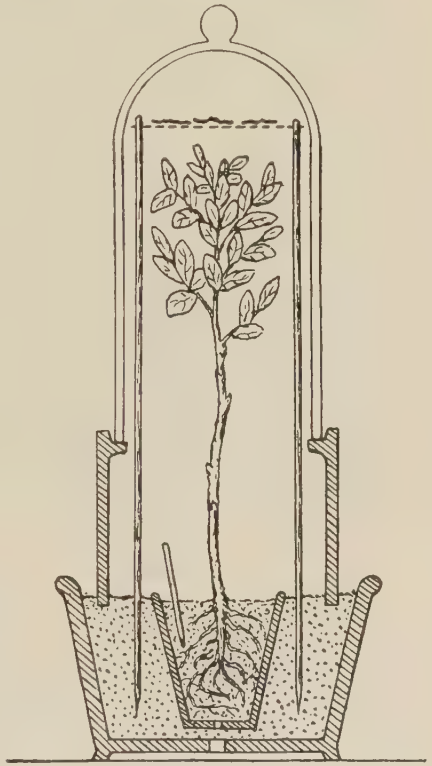


Fig. 183. — Plant growing in a flower pot covered by a bell-jar: the pot is sunk in a vessel containing wet sand, and the bell-jar is raised on a clay cylinder; two stakes support wire or cord on which germinating material is placed. (After Klebahn, 1904a.)

Plant-covers made of wood and glass (Fig. 184), have been found serviceable, and comparatively inexpensive. They are formed from a wooden box without bottom and with a roof-like top made of two sliding sheets of glass. A convenient size is 12 by 15 inches, 8 inches high at sides and 14 inches at center, which will accommodate five or six 3- or 4-inch pots (Mains, 1924a).

Where portions of a large plant are to be inoculated, as for instance the branch of a tree, celluloid cylinders open at both ends are convenient (Fig. 185). The edges of the celluloid are fastened together by applying acetic ether with a small brush, and keeping them under pressure until dry. Moistened cotton is placed inside the celluloid chamber,

Fig. 184. — Inoculation chambers of wood with sliding glass tops. (After Mains, 1924a.)

which is then slipped over the inoculated branch and plugged at the ends with cotton (Hubert, 1916).

When considerable numbers of plants are being treated various types of galvanized iron tanks of capacity to hold a number of potted plants, are convenient. Wet sand or sphagnum in the bottom serves to maintain the necessary humidity (Parker, 1918; Melchers & Parker, 1922a; Mains, 1924a).

One of the difficulties encountered in culturing rusts in the greenhouse is the high temperature which usually prevails in late spring, summer, and early fall. However, by the use of a system of spray-nozzles delivering a fine spray of water, tanks and bell-jars can be kept cool, thus enabling one to conduct culture studies throughout most of the year.

It is usual to leave the inoculated plants in the moist chamber for two to four days, this time being sufficient in nearly all cases to permit infection. With the cereal rusts forty-eight hours is usually sufficient (Stakman & Levine, 1919). It is well to atomize the plants three or four times during this period, especially with a rising temperature, since by so doing the humidity is increased and the chamber is aerated, but it should not be done in a manner to wash the inoculum from the plants.

Fig. 185. — A celluloid inoculation chamber adjusted to a small potted pine. (After Hubert, 1916.)

Care should be taken in removing inoculated plants from the moist inoculation chambers, as the drier atmosphere and sunlight of the greenhouse may prove detrimental. On sunny days the plants can best be removed in the late afternoon, placed beneath the benches or otherwise shaded for a time.

The incubation period (p. 238) of different species of rusts varies considerably. With the majority of species it extends over four to ten days. Usually the first signs of successful infection are small yellowish flecks, and the first indication of sori are small slightly colored dots in the discolored areas. Upon the development of the sori the epidermis is broken and the spores are exposed. With some rusts, especially on woody plants, the incubation period is much longer, extending from a few months to two or three years.

Chambers made partly or wholly of muslin, built upon greenhouse benches, in which the plants are grown either in pots or in the soil of the benches, are especially serviceable in conducting extensive experiments. As the muslin intercepts part of the light it is used as sparingly as possible. The bench is divided every two or three feet with a curtain

of muslin hung from above or supported on a framework. The muslin partitions may be made double better to protect the cultures from stray spores from adjoining chambers (Stakman, Piemeisel & Levine, 1918). In such construction the top, which is usually two or three feet above the bench, rear and front are left open, or are partly or wholly protected by muslin. Glass may be substituted for the muslin, the top being hinged, making a modified Wardian case (Mains, 1924a). If the chambers are large, extending to the roof of the greenhouse, they may be entirely enclosed with muslin and serve not only as inoculation chambers but for the growth of the plants up to the time of maturity (Melhus, Dietz & Willey, 1922).

When a large number of plants are treated at one time with inoculum from a single source, as in testing F_2 and F_3 generations of hybrids, or in a search for resistant strains, a temporary chamber can be constructed by covering the plants with muslin supported by stakes placed in the soil at intervals (Mains, 1926a).

In all chambers constructed partly or entirely of muslin a simple way to lower the temperature and increase the humidity is to wet the muslin occasionally with a spray of water. A particular form of muslin chamber, which is portable and can be used in the greenhouse or out of doors, is an adaptation of the "iceless refrigerator." It is constructed of a skeleton frame of wood, supporting a large pan containing water. Muslin cloths, which have been thoroughly wet, are hung over the sides with the upper ends immersed in the water of the pan. Capillary action keeps the cloths wet, and the evaporation much reduces the inside temperature (Hunt, 1919).

Cultures upon detached branches or leaves. — When not convenient to conduct cultures by using growing plants detached branches or leaves are sometimes employed. A leafy stem thrust into water in a jar or bottle can be utilized for cultures in the same manner as a small growing plant (Arthur, 1906b, 1908a).

Leaves may be placed under low bell-jars, in which the air is kept moist. If it is desired to place more than one leaf under a bell-jar, zinc stands can be used on which moistened glass slides are placed to support the leaves. Only inoculum from one source should be sown under each bell-jar (Farlow, 1885).

Nearly or quite as good results as by any other method can be obtained for the first sporulation after inoculation by the use of Petri-dishes. Water is put into each dish to make a thin layer over the bottom. The leaves to be used are washed with running water, and

one or more placed in each dish while still damp. They are supported by glass rods, rubber bands, or other means, so as not to touch the water and to be near the top when the cover is put in place, but not to touch it. In most instances the leaf should be placed with the upper surface uppermost, if to be inoculated with basidiospores, and with the under surface uppermost, if to be inoculated with aeciospores or urediniospores. The dishes are kept in bright light, in order to promote the health of the leaves and reduce the tendency to mold, but should be screened from the direct rays of the sun. Excessive temperature within the dishes must be avoided. Leaves of firm texture generally remain alive longest. Seven to ten days are usually required to obtain the first sori, but some leaves remain in vigorous condition much longer, even amounting to weeks or even months (Clinton & McCormick, 1924).

Excellent results can be obtained by using a sugar solution in Petri-dishes and floating the leaves on the solution. The leaves should be placed in water immediately upon removal from the plant, and after being thoroughly washed in running water and rinsed in several changes of distilled water are transferred to sterilized Petri-dishes containing only sufficient sterile distilled water to keep the air saturated. The sugar solution need not be sterilized. The sugar solution is added to the dishes forty-eight hours after the leaves have been inoculated. The cultures must have the solution changed every two or three days at which time the dishes are rinsed and the leaves are washed in sterile distilled water. With due care leaves can be kept in good condition for five or six weeks and infection more certainly secured than on the living plants (Waters, 1928).

An inoculation chamber, in which the temperature of both soil and air is automatically controlled, has been described (Peltier, 1923), but is somewhat complicated and costly. Another more extensive device is to construct a dust-proof room in the greenhouse, which can be entered through double doors. It is fitted with a motor and with pipes extending to the outside for changing the air. By drawing the air through a fine spray of water all spores are removed. In such a room it is possible to grow plants in normal health and free of contamination from fungous sources of all sorts (Hungerford, 1920).

There are advantages in making cultures upon plants growing in the open air. Bell-jars can be employed during the inoculation period when the plants are small (p. 379). Sometimes a tent of muslin is used to cover bushes or small trees, and can be managed in such a way as to keep out stray spores (Clinton & McCormick, 1919). Individual cul-

ture chambers have been designed to hold a single large pot or can, and while providing out-door conditions for growth yet guarding against wind-borne spores (Bolley, 1898; Eriksson, 1901–02; Butler & Hayman, 1906).

Isolation of pure strains. — A pure strain of a rust is obtained, as with other fungi, by starting with a single spore. One method is to gently dust urediniospores over a dry plate, or preferably the bottom of a Petri-dish. Under the high power of a binocular microscope places are found where single spores occur well separated from others. These are picked up by touching with a glass rod drawn to a fine point. By this means they are transferred to a leaf of the host. Single sowings are made upon each of a group of young plants in a pot, which is then placed in an incubation chamber. When the first signs of infection show, before uredinia have broken through the epidermis, all the plants in the pot except one are eliminated (Mains, 1924a). The same method can be used with aeciospores.

Another method, which is easier to apply, is to start with a single sorus. This may be done in a number of ways. One way is to lightly dust aeciospores or urediniospores over a pot containing a number of plants of the host. When the resulting sori first appear, and before they rupture the epidermis, one of the plants in the pot is selected which bears only one sorus, and the other plants are removed. If no plant with a single sorus is found, but a leaf is seen bearing a single sorus, the other infected leaves on that plant are cut away and the other plants in the pot removed. Lantern-globes can be used to advantage for establishing pure strains by this method (Mains, 1924a). Another way of securing a presumably pure strain is sparingly to sow the urediniospores from a single sorus, and with the spores from a sorus thus obtained repeat the process. After several repetitions the strain can be considered acceptable (Fromme & Wingard, 1921).

Still another method is to grow the required hosts under aseptic conditions, and to inoculate them with a limited number of spores of known origin. The method, as applied by Ward (1902a) to secure and maintain pure cultures of *Puccinia rubigo-vera* on Bromus, was to sterilize drying towers or large test-tubes in which disinfected seeds of the grass with a mineral nutrient were placed, suitably protected from contamination. In some cases the chambers were aerated by a continuous current of air. The first leaves of the plants thus grown were inoculated with the rust. The method as applied by Mains (1917) is to disinfect kernels of corn (*Zea mays*) with corrosive sublimate and place them in large sterilized

test-tubes along with absorbent paper wet with mineral nutrient. When the resulting plants have developed two or three leaves they are inoculated with urediniospores of *P. sorghi*. The cultures are maintained by transferring to plants grown in the same way, or to plants in lantern-globes.

Exclusion of other fungi. — For most studies it is not essential that saprophytic fungi be excluded from the cultures, since they usually do not flourish on vigorous plants, yet when physiologic studies of the rusts are made, involving the use of nutrient media of various kinds, it becomes important to exclude all other fungi.

Small sections of leaves, which have been grown under aseptic conditions as described in a preceding paragraph, are floated on sugar solutions in small preparation dishes and inoculated with urediniospores taken from a freshly opened sorus. The presence of a sugar solution provides ideal conditions for the growth of saprophytic fungi, and if spores of such fungi are present they will soon develop in a conspicuous manner. By making a series of such cultures some will be found free from saprophytic contamination, and these can be used to establish a pure strain for physiologic or other studies. Another method is to inoculate sparingly the upper surface of leaves with urediniospores, using plants grown under aseptic conditions. As the resulting uredinia usually appear on the under surface of the leaves, they are likely to be free from any saprophytic forms introduced with the inoculum on the opposite side of the leaf (Mains, 1917).

Recording laboratory results. — The method of recording results depends upon the type of investigation under way and the object in view. While in some cases, it is sufficient merely to record whether a plant is infected or not, in most cases other data are of considerable importance. When a study is being made of varietal susceptibility, particularly among cereals, the amount of sporulation and the character of the lesions are of importance as an index to the degree of susceptibility.

In the case of infection from basidiospores necrotic or chlorotic areas may be produced indicating resistance. Pycnia may be formed but no aecia, indicating a somewhat less resistant type. When pycnia and aecia are formed, the number and size of the sori serve as evidence of the degree of susceptibility. In case of infection from urediniospores the result is shown in a somewhat similar manner. Various intergradations are found between an entire absence of visible results and the abundant production of sori.

The length of the incubation period is sometimes important to throw light upon relative susceptibility. It should be kept in mind, however, that the vigor of the host may have an influence. Hosts in an enfeebled condition show more signs of resistance, especially in length of the incubation period, and the number and size of the uredinia, than would be shown by the same hosts when developing vigorously.

The method used in recording these characters varies with different investigators. In some cases the nature of the lesion and the number of sori produced are separately recorded. A scale proposed by Eriksson (1896) has been generally employed with modifications. It divided the amount of infection into four consecutively numbered degrees, ranging from a few sori (1) to full infection (4), the absence of sori being designated by zero (0). This scale has been modified in different ways by various investigators (Jaczewski, 1907, *fide* Naumov, 1923; Litvinov, 1912; Vavilov, 1913; Fromme & Wingard, 1918; Gassner, 1919; Durrell & Parker, 1920; Stakman & Levine, 1922; Melchers & Parker, 1922a; Peltier, 1923; Naumov, 1923; Mains & Leighty, 1923; Hungerford & Owens, 1923; and others), but the basic feature of the varying presence of sori is retained in each instance. Litvinov increased the number of gradations to nine by designating the inserted degrees as 0 to 1, 1 to 2, 2 to 3, and 3 to 4. Other workers have recognized more gradations in the amount of sporulation than Eriksson's original four, and have used an independent series of numbers.

The earlier workers gave consideration almost wholly to the amount of sporulation. Eriksson (1894) at first counted the number of sori produced each day. Litvinov included the number of leaves affected upon each host. Gassner gave attention to the age of the leaves.

The three decades since the beginning of quantitative culture work have witnessed a varied refinement in the observation of results and in the methods of record. But even a greater change has taken place in the attitude of the investigator. For a time at the beginning of the period attention was given chiefly to the objective feature of determining the thoroughness of attack of the parasite as indicated by the number of sori. In later studies there has been added the subjective idea of susceptibility or sensitiveness of the host to the presence of the parasite. The change has been a gradual one, beginning by making each number to include certain characteristics in the appearance of the lesions. Other workers took note of the size and arrangement of the sori, and certain other features indicating the severity of the attack. In this way the numbers have become the index to types or classes of infection, and

stand for varying degrees of resistance and susceptibility. The manner in which such ideas have been incorporated with Eriksson's original four degrees of sporulation is well illustrated in the practice of Mains and Jackson (1926) as given on p. 256. Some investigators have found it advantageous to record still greater refinements by adding to the numbers various letters and symbols, mostly pertaining to the appearance of the rust but partly to that of the host, as a semicolon (;) for flecks and a period (.) for necrotic lesions (Stakman & Levine, 1922).

The size of the uredinia has been found a valuable measure of susceptibility with *Puccinia graminis avenae*, especially under field conditions (Dietz, 1928). The degree of susceptibility is correlated directly with the size of the sori. If there are also small sori intermixed with the large ones, these may be due to some check in the development of the host which reacts upon the growth of the rust, such as approach to maturity.

In addition to written or printed records herbarium specimens, if properly prepared, may be highly serviceable. They are especially helpful when the comparative study of a number of strains must extend over a more or less lengthy period. If leaves of the host are dried rapidly under moderate pressure and with moderate heat, they will retain differences of color and show their various chlorotic and necrotic characteristics for a considerable time (Mains, 1924a).

Good photographs are also important means for preserving records of culture results. The difficulty in making satisfactory photographs lies in the fact that the yellow and orange of the uredinia and of the surrounding tissues give nearly the same photographic effect as that of the green of the leaf. To secure contrasts a Wratten K-2 filter may be used (Peltier, 1923), for greater contrasts Wratten B (green) filter, making red appear black, or for a variety of shades of yellows, browns, reds and greens to be photographed on the same plate the Wratten K-2 and K-3 filters will be serviceable. Photographs taken by transmitted light will supplement those taken by reflected light, as the uredinia will show darker and the chlorotic and necrotic lesions lighter when the light is transmitted.

Field cultures. — Experimental studies conducted under field conditions give valuable information regarding susceptibility of different species and varieties and also furnish clues for the more intensive greenhouse investigations for the detection of strains. It is difficult, however, to arrive at exact conclusions, owing to the vicissitudes of weather and interference from wind-blown spores. To induce infection of

epidemic severity with certainty under field conditions it has been found for the Pacific coast region of the United States that cereals should be sown in July (Mackie, 1928).

The method of planting a field for experimental purposes will depend somewhat upon the kind of plants used in the study and the chief objects in view. The different varieties may be placed in square or oblong plots, either in linear series or in a checker-board arrangement. What is usually a better method, and especially so for cereals, is to sow the varieties in successive rows and replicate the series, if room is available. To neutralize the variations in soil conditions the seeding of the rows should be as uniform as possible, and rows of high and low susceptibility should alternate. By spacing the plants in the row notes can be taken for individual plants.

A sufficient epidemic is generally obtained from the distribution of spores by the wind, especially if the rows of high susceptibility are not too widely separated. Some investigators plant several rows of such a variety around the entire experimental field to assist in providing inoculum. When such methods are not ample pots of rusted plants may be placed at intervals through the nursery.

When studies of the alternate hosts of a particular rust are made, a natural infection may often be secured by mulching between the rows with straw or leaves bearing telia, or scattering such material over the plants.

If natural epidemics fail, either aided or unaided, as they sometimes will under certain unfavorable seasonal conditions, resort may be had to artificial inoculation of the check rows of the susceptible variety, or to dusting or spraying the whole nursery with spores. The dusting may be accomplished by shaking rusted plants over the check rows, or dragging rusted plants through the nursery, or by the use of a blower (Durrell & Parker, 1920). The spraying may be done with an ordinary hand sprayer, using water with spores in suspension (Freeman & Johnson, 1911; Garber, 1922; Melchers & Parker, 1922a).

When the nights and days are dry humidity may be conserved by erecting a wooden framework over the field upon which removable canvas covers are unrolled as required (Melchers & Parker, 1922a).

For details regarding the methods employed by various investigators in planting and utilizing a nursery for the study of rusts reference may be had to the following articles: Eriksson, 1896; Carleton, 1899; Bolley, 1905, 1909; Biffin, 1907; Johnson, 1911b; Freeman & Johnson, 1911; Vavilov, 1913; Fromme & Wingard, 1918; Gassner, 1919;

Durrell & Parker, 1920; Garber, 1922; Melchers & Parker, 1922a; Hungerford & Owens, 1923.

Recording field results. — Similar differences in types of susceptibility occur in the field as in the greenhouse, often, however, not so pronounced. Usually in field work more attention is attracted to the amount of sporulation than to the kind of lesion.

The same scales, or essentially similar ones, are in use for field records as those already described for greenhouse records. A scale in common use in the United States was devised by N. A. Cobb of Australia and later modified and adopted by the United States Department of Agri-

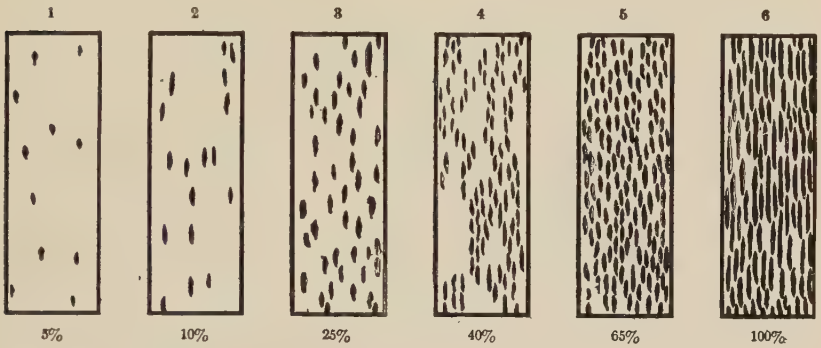


Fig. 186. — Scale in use in the United States for estimating rust. (After Durrell & Parker, 1920.)

culture (Durrell & Parker, 1920; Melchers & Parker, 1922a), which is based upon the degree of sporulation. This scale is standardized by the use of a chart having six divisions, which illustrate 5, 10, 25, 40, 65 and 100 per cent of rustiness (Fig. 186).

To determine the extent to which a variety or a field is rusted the amount of sporulation, estimated on a scale of ten can be multiplied into the percentage of the plants infected. Since 10 is the highest degree of infection and 100 the maximum per cent of plants in the area, 1,000 will thus represent the highest possible attack of rust (Hungerford & Owens, 1923). A much more elaborate method has been devised to accomplish the same end by combining the several factors involved into a formula (Naumov, 1923; Tehon, 1927).

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